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UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*
FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

GULF OF MEXICO

ITS ORIGIN, WATERS, AND MARINE LIFE

Prepared by American scientists under the sponsorship of the
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Coordinated by Paul S. Galtsoff

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PREFACE

The purpose of this book is to summarize in a convenient form the present knowledge about the Gulf of Mexico. Such a summary is needed in connection with a large number of new investigations which are now being conducted in the Gulf of Mexico by Federal and State organizations and private institutions. It is hoped that the background information presented here will be useful to the investigators engaged in the new research projects and will save their time and effort.

Scientific data concerning the Gulf of Mexico have been accumulating since the first explorations in the sixteenth century. They are scattered in thousands of technical publications, some of them rare and not readily available to persons in the Gulf States.

The preparation of a digest of the existing knowledge about the Gulf was suggested by a group of scientists attending, in November 1949, the meeting of the Gulf and Caribbean Fisheries Institute at Miami. The idea, proposed independently by Dr. Lionel A. Walford of the Fish and Wildlife Service and Dr. Waldo L. Schmitt, head curator, Department of Zoology, U. S. National Museum, was unanimously approved, and Paul S. Galtsoff was selected to carry out the project. The magnitude of the task has proved much greater than had been expected. Only through the hearty cooperation of the 55 contributors to this volume has it been possible to complete the work in about 3 years.

For the purpose of this book the Gulf of Mexico is defined as a partially landlocked body of water indenting the southeastern periphery of the North American Continent. Its eastern boundary was drawn from Cabo Catoche at the tip of the Yucatán Peninsula to Key West at the southernmost tip of Florida. This boundary does not constitute a natural barrier; it was arbitrarily determined because of the necessity of restricting the scope of the project. Inland the area under consideration extends to the limits of tidal waters.

The book comprises a number of articles each written by a recognized authority in his field; these are arranged, with minor exceptions, in a taxonomic order following a list of phyla, classes, and orders prepared in 1936 for the American Association for the Advancement of Science and published by Duke University Press. This plan was carried out with the following exceptions: the sections on Rotatoria and Branchiopoda were omitted because of the inability to find anyone willing to review these two groups; and, for the sake of convenience, the articles on parasitic worms were assembled in a single chapter.

A pertinent bibliography is given at the end of each section. A greater number of bibliographical references, comprising more than 4,000 author and subject cards, was prepared in cooperation with Mrs. Margaret M. Quattromini of the Fish and Wildlife Service. The 12 sets of these files have been assembled for distribution among the institutions engaged in research in the Gulf of Mexico. No claim is made that these files are complete, and additional items can be added as new references become available.

In organizing and carrying out the project, splendid cooperation and valuable suggestions were received from the contributors to the book. The writer wishes to express his profound thanks to them for their continuous interest, the great amount of work required to prepare the articles, and their constructive criticism. Waldo L. Schmitt, head curator, U. S. National Museum, and William Randolph Taylor showed unremitting interest in the progress of the work, gave valuable advice in the formulation of the plan, and were most helpful in suggesting some of the authors and persuading them to undertake the review of various groups. My thanks are also due Richard S. Green, Chief, Shellfish Branch, Division of Sanitation, Public Health Service and A. F. Bartsch, biologist, Division of Water Pollution Control, Public Health Service, for organizing the material in the chapter on water pollution; to William S. von Arx of the Woods Hole Oceanographic Institution, Francis P. Shepard of Scripps Institution of Oceanography, Remington Kellogg, Director, U. S. National Museum, Frederick C. Lincoln, assistant to the Director, Fish and Wildlife Service, and Isaac Ginsburg, Ichthyologist, Fish and Wildlife Service, for valuable comments and constructive criticism of certain parts of the book.

The work of Mrs. Margaret M. Quattromini in retyping the text and arranging the bibliographies is gratefully acknowledged.

Paul S. Galtsoff,
Fishery Research Biologist.

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CHAPTER I

HISTORICAL SKETCH OF THE EXPLORATIONS IN THE GULF OF MEXICO

HISTORICAL SKETCH OF THE EXPLORATIONS IN THE GULF OF MEXICO

By PAUL S. GALTSOFF, *Fish and Wildlife Service, United States Department of the Interior*

The brief historical sketch of discoveries and explorations in the Gulf of Mexico presented in this paper is based on published materials available in this country. Fortunately, the large collection of books and maps in the Library of Congress, Harvard University, American Geographical Society, and the Public Library of New York York City provided abundant material from which the progress of scientific knowledge of the Gulf of Mexico could be traced with reasonable completeness. A wealth of data about the earlier discoveries in the Gulf can be found in the classical works of Winsor (1884–89), Thacher (1896), Lelewel (1852), in 20 volumes of history of voyages by Prévost (1746–89), Harrisse (1900), and Fiske (1892).

A student of history of explorations in the New World finds in the writing of Alexander von Humboldt, especially his Examen Critique . . . (1836–39) a rich source of critical information. A catalog of maps of the Spanish possessions published by the Library of Congress under the title, The Lowery Collection (Lowery 1912) not only gives detailed descriptions of maps printed from 1502 to 1820 but also contains a great amount of information about the explorations and cartography of the Gulf. A brief but comprehensive review of the explorations between 1492 and 1543 is given by Kohl (1863).

Many other publications and maps in various institutions in the United States were consulted. The more important of them are the catalog of maps, British Museum (1884, 1885), the catalog of geographical documents in the national library in Paris (Paris, Bibliothqèue nationale, 1892), Phillips' list of maps of America, list of geographical atlases (U. S. Library of Congress, 1901, 1909–20), and the description of Mexican maps by Torres Lanzas (1900). The publications of Phillips are listed in some libraries under his name, while in others they appear only under his titles (see Bibliography); the work of Torres Lanzas may be found under "Spain," "Torres," and "Lanzas." Other references not discussed in the text are listed in the bibliography.

Reports, letters, and other documents written by the earlier explorers show clearly that adventure, military conquest, and search for fabulous riches were the principal impelling forces that lured thousands of men of the sixteenth and seventeenth centuries to embark on the daring voyages beyond the unknown western ocean. Science played only a minor part in these risky undertakings, and scientific observations made in the course of these explorations, which so greatly enhanced the knowledge of the inhabitable world, were merely incidental byproducts of mercenary or military ventures.

History of the discovery and colonization of the New World is beyond the scope of this chapter. The following pages contain, therefore, only a brief summary of scientific achievements of the many explorations in the Gulf of Mexico from the time of its discovery to the present days. The author hopes that the picture of the scientific progress in the studies of the Gulf which he presents here has not been distorted by errors or omissions.

PRE-COLUMBIAN ERA

Written history of the explorations in the Gulf of Mexico naturally begins with the discovery of the New World by Columbus in 1492, but long before the white man set foot on the shores of the islands of America the existence of a large, landlocked body of water now called the Gulf of Mexico was known to the tribes that inhabited its coastal plains and sailed and fished in its waters. Indians living along the west coast of Florida did not venture beyond a narrow coastal zone in which they fished from small dugout canoes. This conclusion is well substantiated by archaeological research in Florida and especially by the study of the contents of numerous shell heaps (Walker 1880, 1885; Wiley 1949), which contain the rem-

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nants of birds, fishes, and mollusks found only in coastal waters.

The Aztecs, who developed their own system of navigation, were fairly well acquainted with certain parts of the Gulf. This is probably true also of the Mexican and Yucatec Indians, who sailed over considerable distances off shore. Evidence for this is given in the report of the fourth voyage of Columbus, who on July 2,1502, sighted a large Indian ship of the size of a Spanish galley about 80 miles east of the Yucatán coast (Kohl 1863).

The art of map making practiced by Aztecs had reached a high degree of perfection as can be judged from the incident described by Bernal Díaz de Castillo (Hakluyt Society Works, 2d ser., No. 24, p. 129, quoted from W. Lowery, 1912, p. 27). During the Cortés invasion of Mexico, he writes, "The great Montezuma gave our Captain a henequen cloth on which were painted and marked very true to nature, all the rivers and bays on the northern coast from Pánuco to Tabasco, that is, for a matter of one hundred and forty leagues, and the river of Coatzacoalcos was marked on it."

For more than 1,400 years of the Christian era the geography of the western world was under the influence of the writings of Claudius Ptolemy, an Egyptian who lived in Alexandria about the middle of the second century (the dates of his life are usually given as between 90 and 168 A. D.), and spent 40 years in making astronomical observations. For many centuries Ptolemy's data on the locations of many places on earth with reference to the parallel of Alexandria were the principal source of information for map makers. No existing Ptolemy maps are known earlier than that of the thirteenth century, the first printed edition of which was executed in 1475 in Vicenza (Thacher 1896).

Some idea of the type of maps available to navigators at the end of the fifteenth and the beginning of the sixteenth century can be gained from examining figure 1 representing the map of the world by Johannes Ruysch, copied from Ptolemy's geography of 1507–08. The discovery of the New World has been already incorporated in it, and the name "Mundus novus" appears for the first time on the engraved map.

During the last 40 years of the fifteenth century the Portuguese seamen made persistent and almost continuous efforts to search for new Atlantic islands beyond the Azores. So far, no documentary proof has been found of the pre-Columbian discovery of western lands by Portuguese, but, as stated by the Portuguese historian, Antonio Baião, " . . . there are numerous indications that the existence of other islands beyond the Azores was known or suspected in Portugal. It was in the wake of these indications that Columbus sailed. His voyage is integrated with cycle of Portuguese explorations of the Western Ocean." (Quoted from Morison, 1940, p. 75.)

Because of the secrecy attached by the Portuguese Government to the discoveries of new lands and their location, the findings of Portuguese seamen were lost, and only inconclusive traces of their efforts remain on certain documents originated in Lisbon. One of these is the famous map by Alberto Cantino which is discussed in the next section of this article (p. 8).

DISCOVERY OF THE GULF OF MEXICO

The discoverer of the New World came almost to the very entrance of the Gulf of Mexico but failed to enter it. On his second voyage, June 1494, Columbus followed the southern shores of Cuba as far as Isla de Pinos, where he stopped. Disregarding the information received from the Indians that the end of the land was not far, he changed his course and sailed eastward. The decision was influenced by his strong belief that Cuba represented the end of the new continent. As it is generally known, he asked his companions to sign a statement to this effect. The declaration, however, was not universally accepted since the earliest maps of the New World by Cosa, 1500 (fig. 3, p. 9), and Waldseemüller, 1507 (fig. 2), show Cuba (Isabella) as an island.

The question who was the first European explorer to sail along the coast of the American continent is by no means settled. The credit is usually given to the man whose name is forever associated with the New World. Amerigo Vespucci, the third son of a Florentine notary, was born on March 9, 1451. He studied diligently and became proficient in astronomy and in the use of the astrolabe, but his principal interest was in a commercial career. After establishing himself as an agent for the House of Cadiz, Vespucci undertook to settle the claims left after the death

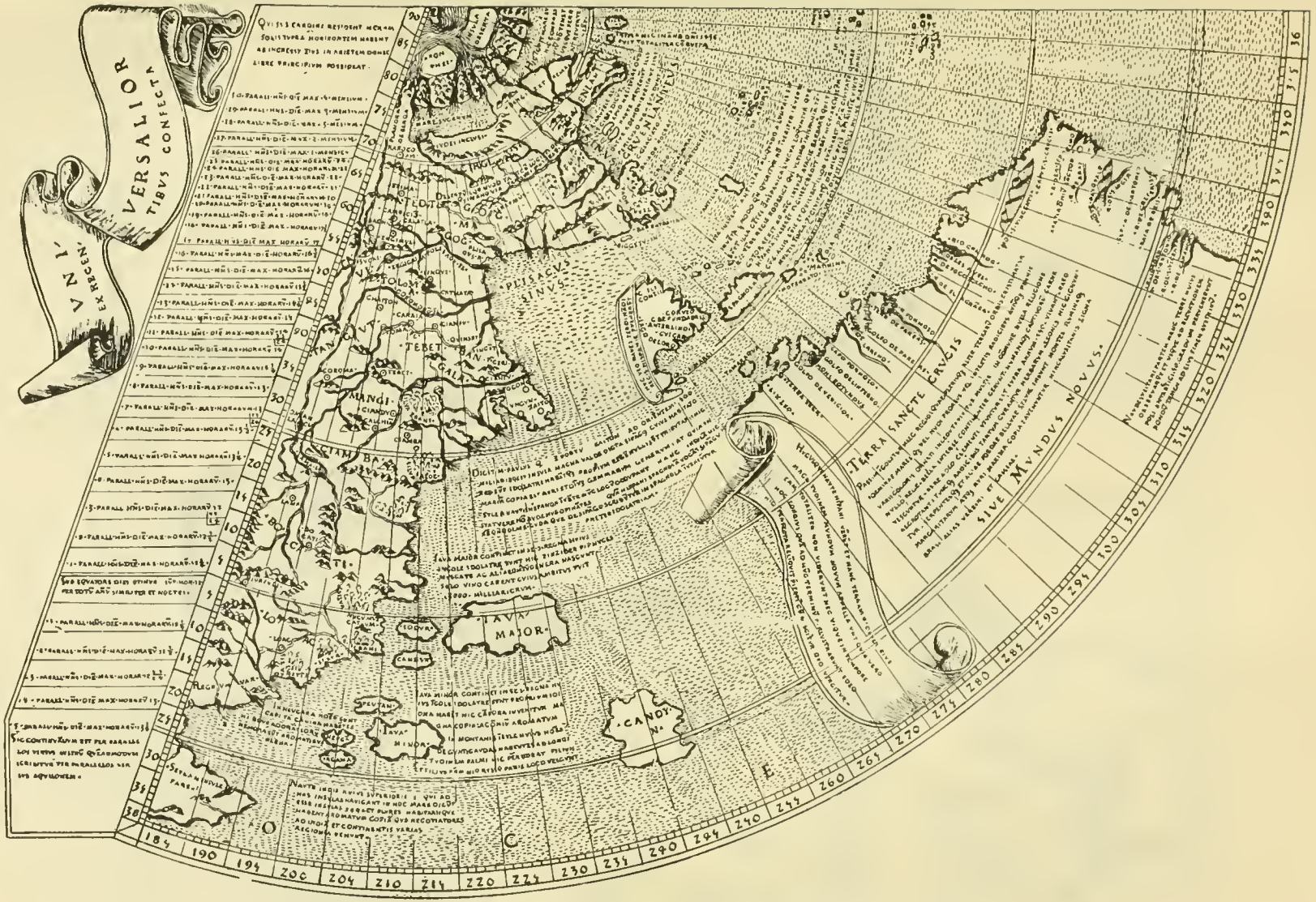

FIGURE 1.—Portion of the world map by Johannes Ruysch from Ptolemy's geography of 1507–08.

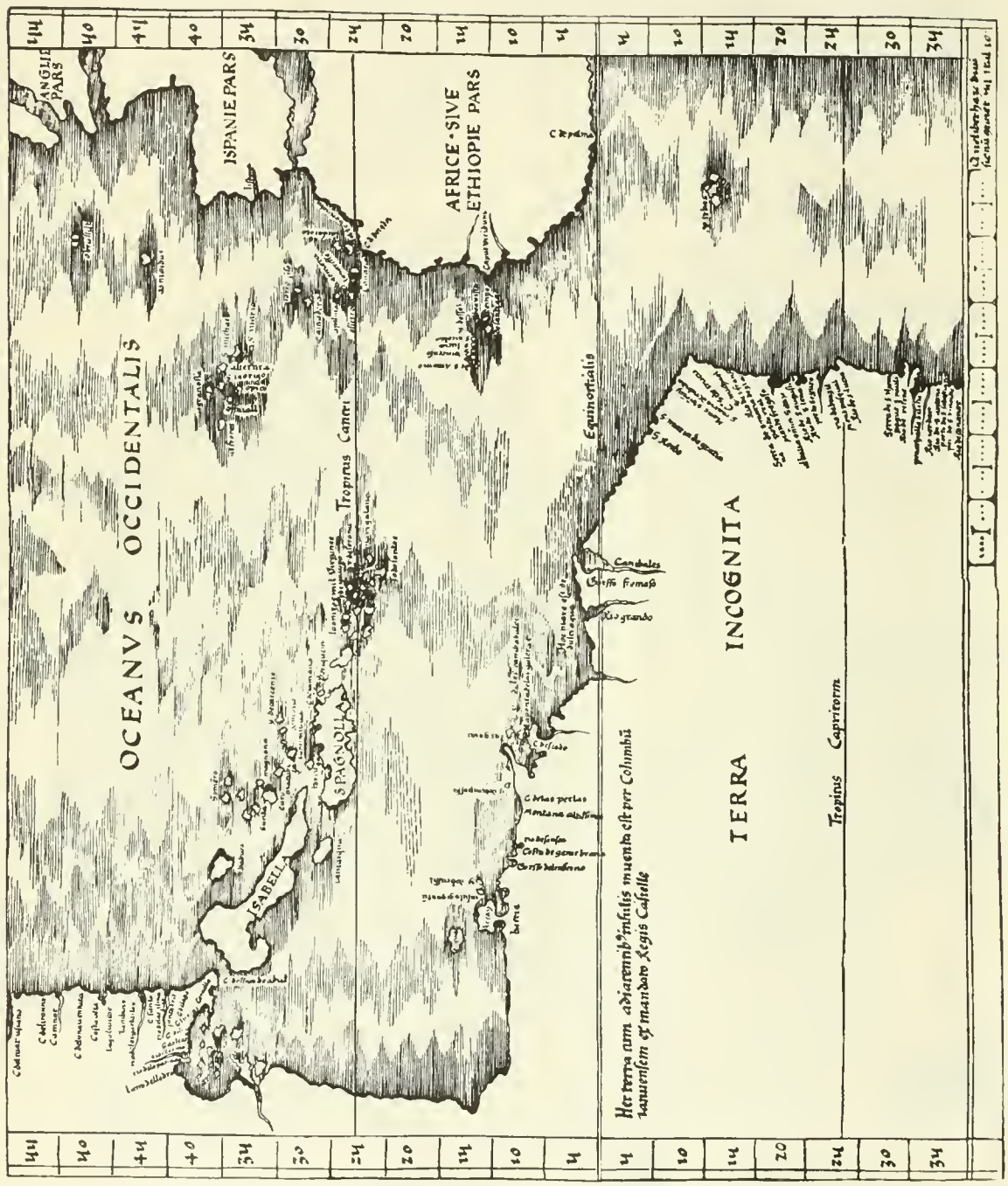

FIGURE 2.—Waldseemüller map about 1507 showing the discoveries of Vespucci, from the Ptolemy geography printed in Strassburg in 1513, known also as the Admiral's map. Reproduction from a copy in the Library of Congress.

of his friend, Juanito Berardi, who contracted to supply and equip 12 vessels of 900 tons each for the Spanish Crown. In 1497, at the request of the king, Vespucci joined the expedition to the New World. In his own words, "the King, Don Fernando of Castile, being about to dispatch four ships to discover new lands toward the west, I was chosen to aid in making discovery" (Thacher 1896, p. 69). He never explained his exact duties aboard the ship, but judging from his previous experience in commercial methods he probably went as a sort of supercargo to supervise the distribution of food, to weigh the gold, and to keep accurate tally of the Crown's share which, according to the royal decree of 1495, was one-third of the total gold obtained by the expeditions.

Vespucci started from Cadiz on May 10, 1497. After reaching the Canary Islands in about 10 days, the fleet sailed west and quarter-southwest for 37 days (27 days according to the Latin text of Vespucci's letter) until land was sighted a thousand leagues from the Canaries. Making allowance for an error of 1° latitude and about 8° longitude, Thacher (1896) estimated that the landfall would be off the coast of Honduras in the vicinity of Cabo Gracias a Dios. It is interesting to note that the ships passed between the islands of the Caribbean without noticing them. A safe harbor was found after 2 more days of sailing northward. Vespucci describes how, skirting the coast, he saw villages one of which, consisting of 40 houses, was built, like Venice—upon the water. It was near this village that a fierce encounter with Indians took place in which 15 or 20 natives were killed. The place is probably on the shores of Campeche Bay, north of Tabasco.

Continuing for 80 leagues farther along the coast, the expedition came to a place inhabited by different people. It was called the Province of Lariab, a name which later on caused a great deal of confusion and argument since in the Latin edition of Vespucci's letter the name was translated "Parias," a mistake that led many to believe that the explorer referred to the Gulf of Paria off the Venezuelan coast discovered by Columbus in 1498 during his third voyage. According to Thacher, the word "Lariab" is a compound word of Quiche dialect which means "there are many." It is assumed that the expression was used by the natives, who misunderstood the question addressed to them by Spaniards about the name of their province and answered that there were many people in the land. Vespucci states that this land, which is probably near Tampico in Mexico, is "within the torrid zone, close or just under the parallel described by the Tropic of Cancer where the pole of the horizon has an elevation of 23° at the extremity of the second climata." (Quoted from Thacher, 1896.) The term "clima" (plural "climata") of ancient Greek cartographers denotes parallel zone or belt, the width of which, according to Hipparchus, is determined by astronomical observations on the basis of the longest day of the year.

The rest of the letter (Vespucci, 1926 edition) caused endless arguments among geographers. Vespucci states that from Lariab they navigated in sight of land and covered 870 leagues, still going in the direction of the "maestrale." This course, corresponding to northwest, would have brought the expedition over the continent nearly to the coast of California. Harrisse (1900) ignores the western component of the direction of "maestrale" and considers only its northerly meaning. He states that plotting 870 leagues along the American coast would bring Vespucci's ships as far north as Cape Hatteras. According to Vespucci's narrative, the expedition turned east toward Bermuda from this place and returned to Cadiz on October 15, 1498.

Humboldt (1836–39) expresses doubt whether Vespucci ever made this voyage and denies him the credit of discovery of the new continent. According to Humboldt, at the time of his supposed voyage Vespucci was engaged in equipping the third expedition of Columbus and could not possibly have taken part in the explorations he describes. Obvious inconsistencies in the text of Vespucci's informal letters are unfortunately augmented by errors in translation. The accusations that Vespucci was a fake (see Winsor 1886, v. 2, pp. 129–136; Harrisse 1895) are answered, however, by pro-Vespuccian writers (Varnhagen, 1865, 1869a, 1869b, 1870), and final settlement of the question awaits further historical research.

Bremer (1940) advances an entirely new theory that the honor of the discovery of the Gulf of Mexico belongs to a Portuguese by the name of Gaspar Corte Viall who, shortly before 1500, sailed to the west and upon returning to Portugal spread the news of the existence of a new continent and islands in the western ocean. In support of his

hypothesis, Bremer mentions a place on the northern coast of the Gulf of Mexico known by tradition as Portuguese Field, which he considers may be a landing place of Portuguese sailors. The evidence, however, is not convincing.

SIXTEENTH AND SEVENTEENTH CENTURIES

The progress of early discoveries in the Gulf may best be followed by studying the maps of this period. Since the data concerning the location of new lands were considered by the Spanish Government a state secret, maps and reports which the captains of the ships were requested to submit to the government immediately upon their return to Spain were carefully guarded, and all means were taken to prevent them from falling into the hands of other European powers. As a consequence of this policy of secrecy the first maps of the New World were engraved and published outside Spain (in Italy, France, and Germany), using data which were often surreptitiously obtained or smuggled out of the country. Many of the original documents, usually drawn on parchment or oxhide, were lost or destroyed in war and by accidents; only a few of these valuable documents were recovered in more recent years after many vicissitudes.

The first map of the world summarizing the discoveries in the western ocean and showing the Gulf of Mexico was drawn by Juan de la Cosa, the companion and pilot of Columbus and owner of the caravel, *Santa Maria*, which bore the admiral's flag and was the first ship to reach the New World. The map embodies the results of seven important voyages: the three voyages of Columbus in 1492, 1493, and 1498; the first and second voyages of Vespucci in 1497 and 1498; and the first and second voyages of Cabot in 1497 and 1498. The date of the execution of the map is established by the inscription which reads, "Juan de la Cosa el fiso en el porto de *Santa Maria* en año de: 1500."

The history of this unique historical document is interesting. After being lost for three centuries, the map was found in 1832 in a Paris bric-a-brac shop where it was purchased for a small sum by Baron de Walckenaer. Its great significance was pointed out by Humboldt (1836) when in 1832 he drew public attention to its importance. After the death of Walckenaer the map was offered for sale at public auction and was purchased for 420 francs by the Hydrographic Department of the Spanish Government. Today it hangs in the Naval Museum of Madrid, listed in the museum guide book as number 553, with a detailed description and a brief history of this remarkable document (Madrid, Museo Naval, 1945).

The original map is drawn on oxhide, 5 feet 9 inches long, cut square at the tail of the hide where its width is 3 feet 2 inches. The Tropic of Cancer runs vertically through the middle; the top corresponds to the extreme west and includes the Caribbean Sea and the Gulf of Mexico. The latter area, instead of geographical details, is occupied by a rectangular drawing representing St. Christopher bearing the Christ child, a rather crude imitation of the famous woodcut engraving of 1423. Originally the map was rich in blue and gold and illuminated after the fashion of medieval manuscripts, but today it is torn and faded. Peter Martyr, who saw it in 1514 in the house of the Bishop of Burgos, head of the Maritime Department of the Casa de Contratación, remarked on its highly colored beauty.

The photographic reproduction of the Cosa map available in the Library of Congress is too blurred and cannot be clearly copied in the text. The part of the map referring to the Gulf of Mexico can be seen in figure 3, representing a copy found in volume 4 of Humboldt's Examen Critique (1836–39); this part of the map was redrawn and oriented by Humboldt in the conventional manner.

One of the earliest documents showing certain details of the New World and a part of the Gulf of Mexico is Cantino's map of the world. It represents for the first time what appears to be the west coast of Florida and the adjacent part of the Gulf (fig. 4). It was drawn as a large planisphere on parchment in gold and various colors. The map derives its name from Alberto Cantino, Ambassador of the Duke of Ferrara to the King of Portugal. The original, located in Biblioteca Estense in Modena, was obtained by Cantino for 12 ducats and was sent by him with a letter to Señor "Duca Hercole" in Lisbon. In later years the map was used as a screen and finally was recovered in a damaged condition from the shop of a pork butcher in Modena and deposited in the library.

Some cartographers (see Lowery 1912, pp. 5–6)

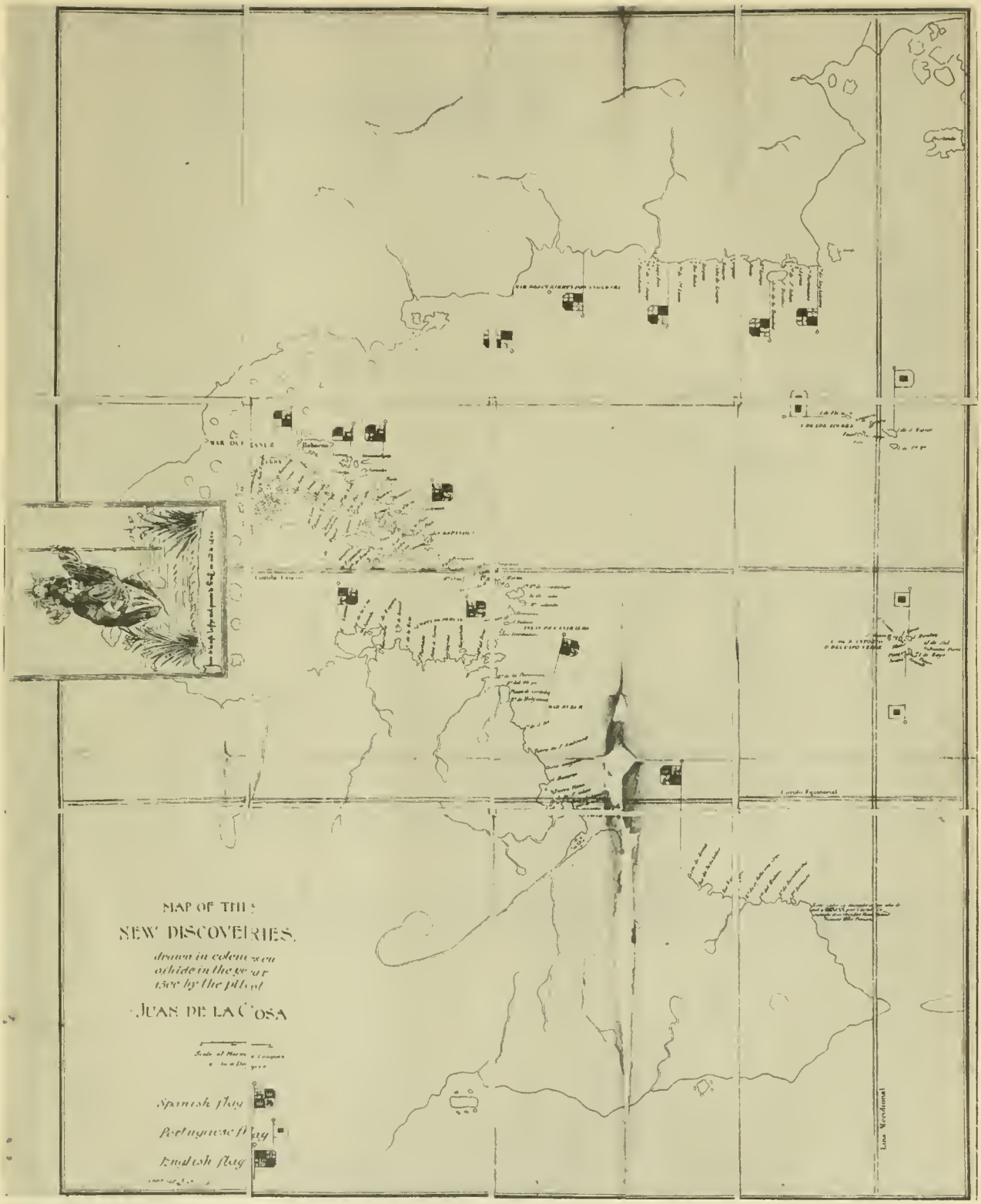

FIGURE 3.—Western part of the map of the new discoveries drawn by Juan de la Cosa. Reproduced from a copy in Humboldt's Examen Critique (1836).

FIGURE 4.—Western portion of the Cantino map of the world, 1502. Original without name, date, or title. Reproduced from a copy in Harrisse's Les Corte-Real 1883.

consider that Cantino was familiar with the Portuguese voyages to the New World and incorporated their discoveries in his drawing. This subject, as well as the questions whether "Ilha Ysabella" on the map represents the island of Cuba or the Crooked Islands group called "Isabella" by Columbus, and whether the peninsula west of it is Florida, are critically discussed by Morison (1940).

The Gulf of Mexico is very crudely shown on the map of the world made by the German cartographer, Waldseemüller, and printed in 1507 in St. Dié, Lorraine. This map is famous because for the first time the continent of the New World is shown with the name "America" attached to it in honor of the Florentine explorer. The original is owned by Franz Joseph II of Liechtenstein.[1]

Of the many expeditions that sailed to the New World during the first decade of the sixteenth century, the more important ones were those headed by Hojeda, 1499; Niño and Guerra, 1500; Pinzón, 1499–1500; Lepe, 1500; Bastidas, 1500–02; Hojeda and Vergara, 1502–03; and Cosa, 1504–05. Results of these ventures materially enlarged the knowledge of the geography of the eastern part of the Caribbean area, but its western section, including the Gulf of Mexico, remained unexplored.

In 1513 the expedition headed by Ponce de León made a formal discovery of Florida, the existence of which was probably known to Spanish and Portuguese adventurers who visited the land north of Cuba but left no records of their findings. On Easter Sunday, March 27 of that year, Ponce de León with his three ships was in sight of land not far from the present city of Jacksonville. To commemorate the holiday the land was named la Florida. Failing in his attempt to circumnavigate the "island" Ponce de León turned south and on May 12 of the same year found a chain of islands which he named las Islas de los Mártires (present Florida Keys), and about a month later he discovered the Tortugas. In the following year, 1514, the King of Spain incorporated the newly discovered land in an administrative region known as Adelantado de la Isla Bimini e la Florida.

Ponce de León was the first explorer who recorded the existence of a strong current along the east coast of Florida. He reported that his ships' while crossing the stream near Cape Canaveral, frequently were swept by strong current. He obviously was referring to that part of the Gulf Stream which at present is known as the Florida Current (Herrera 1601, 1728; Stommel 1950).

In 1516 Diego Miruelo undertook another expedition to Florida, and in the following year, 1517, Fernando de Córdoba and Antonio de Alaminos explored the northern and western coasts of Yucatán. Driven for several days by a severe storm they finally saw land with a large Indian town, near Cabo Catoche. The expedition recorded many points, bays, and harbors along the west coast of the Gulf and safely reached the Bay of Campeche, giving it its present name. Trouble started, however, near the place called Champoton where Córdoba and his landing party were attacked by Indians. In this encounter, Córdoba was badly wounded and many of his soldiers were killed. Alaminos, the principal pilot of the expedition, decided to take advantage of the prevailing easterly winds and sailed north to Florida and then turned south toward Cuba. His decision was a right one. In a few days the ships crossed the Gulf and returned to Cuba, where Córdoba died of his wounds.

Scientific results of the expedition were significant. More than 500 miles of the Gulf coast were mapped; proof was obtained of the existence of an open channel between the Florida and Yucatán Peninsulas; and valuable information was accumulated regarding the prevailing winds, currents, and depth of water. Alaminos was still under the impression that Yucatán was an island. The name Yucatán was taken from the expression "Uyucatan" which the Spaniards frequently received from Indians in reply to their questions, the meaning of which was "we don't understand you."

Before his death, Córdoba appointed his nephew, Juan de Grijalva, commander of a force consisting of 4 ships and 250 men. Experienced Antonio de Alaminos was again the senior pilot of the expedition which on April 20, 1518, sailed from the harbor of Matanzas (Cuba) and followed Córdoba's former route toward the Cape of Yucatán. Stormy weather drove the expedition farther south along the eastern coast of the peninsula toward an island called by the Spaniards la Isla de Santa Cruz but known at present as Isla de

[1] In May 1950 the map was offered for sale at an auction in New York City with the condition that bids should exceed $50,000, but in the last minute was withdrawn by the owner.

Cozumel. From this point the ships turned north around the Yucatán Peninsula and on May 26 passed the point reached by the previous expedition and entered a large bay which was called Boca de Términos (Laguna de Términos on modern charts). Grijalva thought that he had reached the end of the Yucatán island which he named La Isla de Santa María de Remedios, the name which appeared on maps of that time. The expedition continued along the unknown coast for nearly a thousand statute miles to a point a short distance south of the present location of Tampico.

Grijalva's expedition substantially contributed to our knowledge of Gulf geography. The names of many familiar places such as Grijalva River, the bay and river of Tonola, Coatzacoalcos River, Alvarado River, and many others were established and their positions indicated on maps. Alaminos made many astronomical observations between Yucatán and Tampico. Some of his determinations of latitude—for instance, that of a small island where the present town of Veracruz is located—were accurate within 1°. He also observed and recorded the currents along the coast and made soundings and other hydrographical observations.

When the expedition entered the mouth of the Grijalva River the Spaniards were encountered by many Indians having gold in their possession. When asked for the name of the land the metal came from, the Indians replied, "Mexico." In this way the Spaniards heard for the first time the name of the country which played such an important role in the expansion of Spanish power in America.

Upon reaching his farthermost point at Pánuco, Grijalva became convinced that he was exploring the coast of a large continent and not of an island as he had first believed. Realizing the importance of this discovery, he dispatched Pedro de Alvarado on a fast ship to inform Governor Velásquez of Cuba of his important finding and sailed back following the same route the expedition took from Cuba.

A new expedition organized by Velasquez in 1519 was in command of Hernando Cortés with Antonio de Alaminos again serving as chief pilot. In May of the same year the expedition sailed around Cape Catoche, following in general the route taken previously by Grijalva. This time the Laguna de Términos was explored more carefully by Captain Escobar who established its true nature as a shallow, landlocked body of water not suitable for establishing a colony on its banks. Antonio de Alaminos, who was sent northward to Cabo Rojo south of Tampico, discovered a large river emptying into the Gulf and named it Rio Grande de Pánuco.

Besides the surveys of the coast from Cape Catoche to Tampico, Alaminos' principal contribution to the exploration of the Gulf was the discovery of a free passage between Florida and Cuba which represented the shortest route for Spanish vessels carrying silver from Mexico to Europe.

In 1519 Francisco de Garay, Governor of Jamaica, sponsored an expedition of Don Alonzo Álvarez de Pineda to explore the northern coast of the Gulf. Four ships provided by Garay sailed from Jamaica toward Florida. Believing that Florida was an island, Pineda followed the west coast looking for a passage and, not finding it, turned west along the northern coast of the Gulf. In the course of his exploration he discovered the mouth of the Mississippi River which he called "Rio del Espiritu Santu" and described the body of water east of the delta as "Mar Pequeña" or a small sea, the name of the present Mississippi Sound which persisted on many charts for nearly two centuries. Pineda noted the physiographical character of the shoreline, recorded the positions of dunes, low-lying sandspits, bays, knolls, marshes, and oyster banks (*ostiales*) which abounded in the Mississippi Sound and in the delta of the Mississippi River. He realized that the majestic freshwater stream which he ascended for several miles must originate on a large land area, and other observations convinced him that he was exploring the coast of a great continent.

Although the majority of writers agree with Harrisse (1900) that the river Pineda named Rio del Espiritu Santu is the present Mississippi River, there are others who think that the description of the country given in his reports does not agree with that of the mouth of the Mississippi and that Pineda's expedition actually was in Mobile Bay (Scaife 1892). This question probably never will be answered with complete certainty. As a result of his explorations Pineda produced several new maps showing, with approximate accuracy, the outlines of the Gulf coast. Only one of them, bearing the title "Traza

de Costas de Tierra Firme y las Tierras Nuevas," was published. The original, dated 1521, is in the Archivo General de Indias, in Seville, and its reproduction is given by Navarrette (1837) and Winsor (1884, v. 2, p. 218).

In 1521 the west coast of Florida was revisited by Ponce de León, who landed probably in Charlotte Harbor where he was seriously wounded in a battle with Indians. He died within a few days, after being taken back to Cuba. This expedition added nothing to the progress of geographical knowledge of the Gulf.

The next attempt to conquer Florida and explore the northern part of the Gulf was made by Pánfilo de Narváez, who had distinguished himself in the conquest of Cuba under Velásquez and was at the head of an expedition sent by the Spanish Government to compel Cortés to relinquish his command in Mexico. His defeat and imprisonment by Cortés did not reflect on his reputation, and upon returning to Spain he obtained from Charles I a grant to colonize a vast expanse of land from Florida proper as far west as Rio Pánuco.

On June 17, 1527, five ships under the command of Narváez sailed from San Lucas, Spain, with 600 men and officers aboard. One of his companions was Cabeza de Vaca, the treasurer of the fleet. After leaving the south shore of Cuba in March 1528, the ships, driven north by strong winds, found shelter in a large bay which the Spaniards called Bahia de Santa Cruz. According to the description given by Cabeza de Vaca, the bay extended from 7 to 8 leagues inland, had many islands, and presented an excellent anchorage with a depth of water of about 6 fathoms. There is no doubt that it was the present Tampa Bay.

Misinformed by Indians that the land north of the bay, known as Apalachee, was rich in gold, Narváez marched overland with 300 officers and men while his ships under the command of Miruelo followed the northern direction along the coast. The rendezvous was supposed to be in a bay north of the point of their departure.

In about 2 months, Narváez's column reached the village of Apalachee where with great difficulty the men found only a few bushels of corn. Trying to establish contact with the ships, Narváez turned south and discovered a river, Rio de Magdalena, as the Spaniards called it, which probably corresponds to the present Apalachicola River. The party suffered many hardships in the swamps of this region, and many men perished of exhaustion and disease.

Failing to contact the ships, Narváez decided to march west rather than to return to Tampa Bay. On the shores of a bay, which probably corresponds to the present St. George Sound and which was named Bahia de los Caballos, the Spaniards were compelled to slaughter their last horses to make crude boats of their skins, and sailed westward. They followed the shoreline, entering different lagoons (Pensacola, Santa Rosa, and others). In November they reached a bay with many islands (probably Chandeleur Sound in the Mississippi Sound). Since the water was fresh they realized that they were near the mouth of a great river which they attempted to enter, but strong wind and current drove them into the sea where Narváez perished in the storm. His companion, Cabeza de Vaca, found refuge on a small island 5 leagues long and 2 leagues wide which he named Isla de Malhado. The place may be Ship Island, Horn Island, or some other island in the Mississippi Sound.

Scattered by the storm, most of Narváez's men perished. With a few men, Cabeza de Vaca succeeded in landing on the mainland, where for 6 years he lived among the Indians. In 1533 he gave up hope that any European ship would visit the coast and with Lope Oviedo decided to march westward. Encountering a few small streams they came to the banks of a very large river which they considered to be Rio del Espiritu Santu (Mississippi River), and after crossing it marched for a long time through Texas until they reached the Bay of California.

In 1536 Cabeza de Vaca returned to Europe where the results of the unfortunate expedition became known. Its principal scientific achievements can be briefly summarized as follows: The Mississippi River was seen for a second time; Tampa Bay was more fully explored, and new names, such as Apalachee Bay, were added to geography.

After waiting in vain for Narváez at the place of rendezvous, Miruelo returned with his ships to Tampa Bay. It is interesting to note that, although he failed to reach the bay at the north coast of the Gulf where he was supposed to meet Narváez, the name of Bahia de Miruelo

appeared for many years on the charts in the place of the present Apalachee Bay.

Shortly after the tragic end of the Narváez expedition, Fernando de Soto, a Spanish captain and explorer, was preparing for a new adventure. De Soto acquired a large fortune from the conquest of the Inca Empire in Peru in which he played a prominent role. He obtained from Charles V a commission as "Adelantado" of the lands of Florida and Governor of Cuba and invested his large fortune in a new adventure.

On May 18, 1539, seven ships comprising De Soto's flotilla carrying 700 soldiers, 200 horses, mules, supplies, and materials, sailed from Havana. On May 25 they reached Tampa Bay, known as Bahia de Espiritu Santu. From Tampa Bay, De Soto with a large detachment of horsemen and foot soldiers went by land to Apalache. One of his companions, Juan de Añasco, a prominent seaman, cosmographer, and astronomer was engaged in making scientific observations during this military expedition. After reaching the land north of Apalachee, De Soto despatched Añasco south to find a harbor. During this travel the party discovered the bones and other remains of Narváez's men, and coming finally to the shores of the sea discovered a large bay which they called Bahia de Aute (present Apalachee Bay).

In January 1540, De Soto ordered Captain Diego Maldenado to sail for 100 leagues along the coast to take records of all the bays, harbors, and rivers and to return in 2 months. In the course of this survey Maldenado found a bay 60 leagues west of the Bay Aute which he described as the most beautiful harbor in the world ("un hermosissimo puerto"), protected against all winds. He named it Achusi. The entire harbor was sounded with great detail, for De Soto wanted to use it as a rendezvous and a base for his operations. Detailed descriptions made by Maldenado leave no doubt that Achusi corresponds in every respect to the present Pensacola Bay.

After exploring the east coast of the American continent as far north as the Savannah River, De Soto returned to the Gulf and in October 1540 investigated the place called Mavill or Mauvill which is the present Mobile. His further explorations lead him inland and westward to the banks of the Mississippi which he crossed at Chickasaw Bluffs near the present location of Memphis, Tennessee.

In 1542 he died and was buried at the bottom of the Mississippi River. Before his death he appointed Luis de Moscozo de Alvarado as his successor.

After many vicissitudes the Spaniards, under the leadership of their new chief, constructed several boats in which they sailed down the river, successfully evading the pursuit of Indians. Upon reaching Gulf waters they turned westward with the hope of landing somewhere on the Mexican coast. All navigation instruments were lost when the Indians burned the Spanish camp at Mobile, but one astrolabe was saved by Añasco. Being a careful and resourceful man, he managed to make a sea chart from a parchment of deerskin, and with a forestaff, made from a ruler, and an astrolabe salvaged from the fire at Mobile, attempted to guide the course of the flotilla. His worthwhile efforts were so much ridiculed by the other seamen because Añasco had never before embarked on any other maritime expeditions, that in disgust he threw his instruments, except the astrolabe, into the sea.

One day, because of bad weather, the ships sought refuge in a small cove. While some of the Spaniards were gathering shellfish along the shore they found some slabs of black bitumen almost like tar which the ocean had cast upon the beach. Garcilaso, who tells this story (Garcilaso de la Vega, Varner's translation, 1951, p. 601), says, "This substance must come from some spring which flows into the sea or which is born in the sea itself. The slabs weighed 8, 10, 12, and 14 pounds; and they were found in quantity." The tar-like substance was successfully used by the Spaniards to repair the leaky vessels, and after spending a few days on the shore they continued westward. This is probably the earliest reference to the finding of asphalt along the Gulf coast. After many days of sailing along the coast line Moscozo entered the mouth of the Pánuco River and landed in Mexico.[2]

The discovery of Pensacola Bay, exploration of the delta of the Mississippi River and of the northern coast of the Gulf, and the convincing evidence that the Mississippi was a mighty stream draining from a large continent, were the principal scientific contributions of the De Soto expedition.

[2] Detailed account of De Soto's expedition can be found in the report of the U. S. De Soto Commission (1939).

Its unhappy completion marked the end of the period of the earliest explorations in the Gulf.

Sixteen years after the return of Moscozo a Spanish conquistador, Don Tristan de Luna, organized a new expedition to the Gulf. This expedition contributed little to the science of geography. By this time Spain's interest in the new land across the ocean and the enthusiasm of her rulers for new explorations and colonization of the New World somewhat slackened.

Although the great advantages derived from the possession and colonization of the newly discovered territories were fully appreciated by the Spanish Government and by the educated class of the Spanish nation, the country lacked ability and resources to develop them. At the same time, the Spanish Government jealously watched the efforts of other nations to establish themselves in the New World. It tried by every means to prevent French colonization of the country surrounding the Gulf of Mexico and did not hesitate to send military expeditions to destroy French colonies.

The results of many expeditions in the Gulf conducted during the first half of the sixteenth century provided the cartographers with new, reliable material for the construction of new maps, and consequently, the outlines of the Gulf shown by them in their drawings began to assume more or less correct configuration. This can be noticed, for instance, by examining figure 5, representing Mercator's map of 1538, in which for the first time the name America was applied to the entire western continent.

It may be of interest at this point to make a brief survey of the geographical names which were given to the Gulf of Mexico. No special name for the Gulf is found on the map of Juan de la Cosa of 1500 or the Waldseemüller map of 1507, although in both of them the location of the Gulf is clearly shown. Cortés, in his despatches, referred to the Gulf as Mar del Norte, while the names Golfo de Florida and Golfo de Cortés are found in the writings of other explorers. The name Sinus Magnus Antilliarum appears on an old Portuguese map made in 1558 by Diego Homen (original in British Museum). Probably the most remarkable name is that of Mare Cathaynum (Chinese Sea) which is found on one chart of the middle of the sixteenth century (copy reproduced in the Mémoirs de la Societé de Nancy, 1832). In 1550 the name Golfo de Mexico appears for the first time on the world map the original of which, according to Kohl, is in the Bodleian Library in Oxford. Earlier Spanish geographers used, also, the name of Golfo de Nueva España. Herrera (1728) called it Ensenada Mexicana and Seño Mexicano, the names which persisted in Spanish admiralty charts until the eighteenth century. The present name, the Gulf of Mexico, and the corresponding names, Golphe du Mexique in French and Golfo Mexicano in Spanish, appear to have been in use since the middle of the seventeenth century.

During the latter half of the sixteenth century the French Huguenots, trying to escape religious persecution in Europe, made many attempts to establish colonies in Florida. Their efforts were primarily directed to the east coast of Florida where the French penetration lead to many bloody encounters with the Spaniards. Probably the most significant French contribution to geographical knowledge of this time was Le Moyne's map of Florida. Jacques Le Moyne de Morgues was an artist who accompanied a French expedition to Florida under Laudonnière in 1564. His map shows only a part of the Gulf of Mexico east of the Mississippi River. Since it is known that French observations were limited to the east coast of America between the point south of St. Augustine and Rio Jordedan (Charleston Harbor) in the north, the rest of the map was obviously borrowed from Spanish sources. The names of many places are corrupted as, for instance, Apalache Bay is indicated as Sinus Morquel, corrupted from the Bay of Miruelo, and the Bay of Ponce de Leon (Tampa Bay) is called Sinus Joannis Ponce. This map, published by De Bry in 1591 after the death of the artist, was for 50 years copied by Dutch and French cartographers but was completely ignored by the Spaniards.

Le Moyne produced, also, a series of extraordinarily interesting drawings depicting the home life, habits, methods of hunting, and ceremonies of the Timucua Indians. Excellent reproductions of these illustrations together with a translation of the Latin text of De Bry were published in English (Le Moyne, 1564, ed. 1875) and some of the drawings are reproduced by Swanton (1946, tables 51, 53–57, 81, 82, 85, 87, and 106). Examination of these illustrations gives an insight into the tribal life of Florida

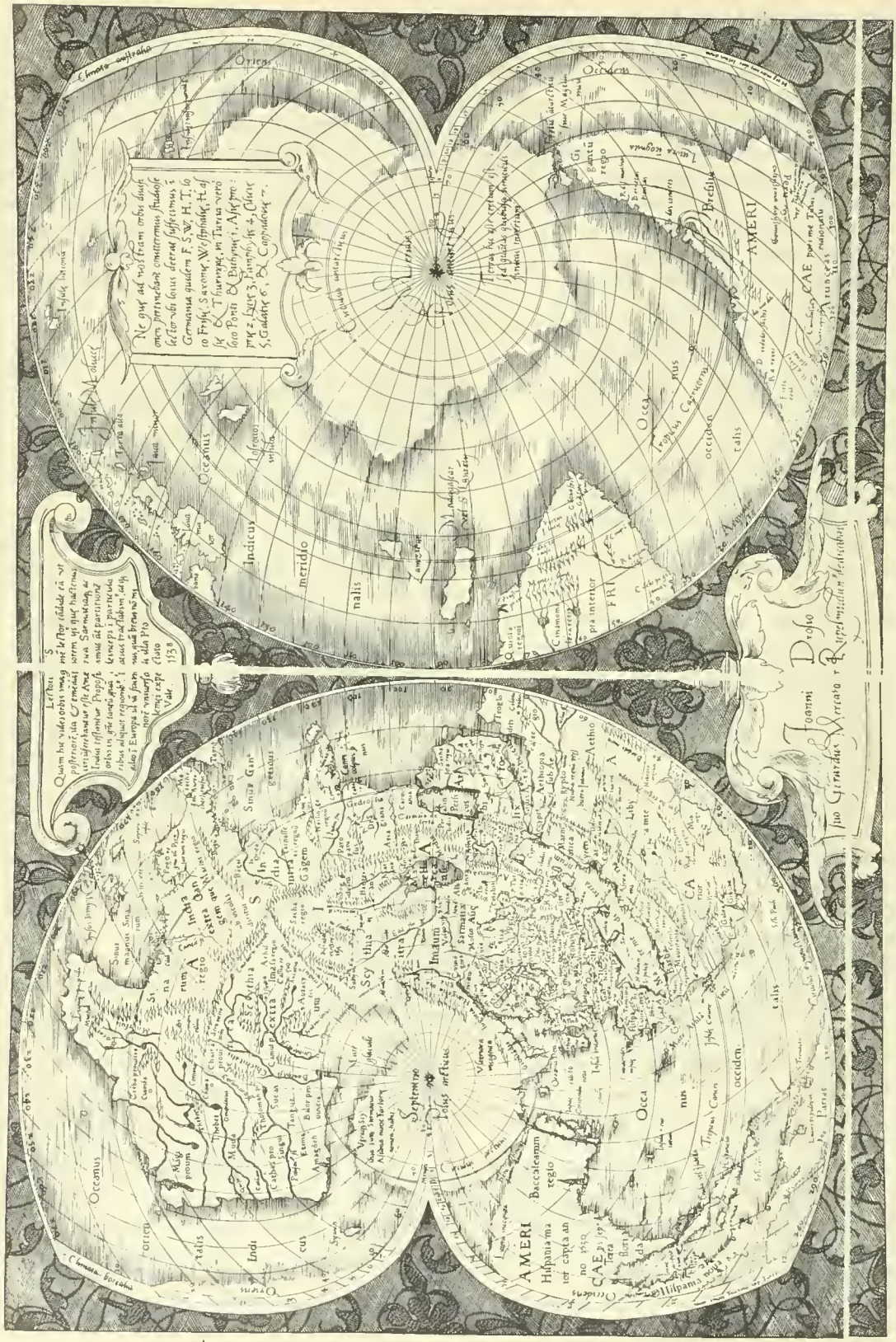

FIGURE 5.—The Mercator map of 1538. Reproduced from a copy in the Library of Congress.

Indians as it was interpreted by a French artist. Particularly amusing are the scenes of alligator hunting in which the beast exceeds many times its normal size and the peaceful scene of the Timucua Indian women sowing their fields, the latter drawing conveying a bucolic atmosphere in conformity with the prevailing artistic taste of that time.

No significant advance in geographical knowledge of the Gulf was made during the latter part of the sixteenth and the first half of the seventeenth century. In this period Spanish ships loaded with gold and silver continued to sail from Mexico to Havana following the northern coast of the Gulf and passing the delta of the Mississippi River which was called Cabo de Lodo, or Mud Cape. The names of the earlier discoverers, such as Pineda, Narváez, Ponce de León, De Soto, and others whose exploits made possible the relatively safe sailings of these ships, were almost forgotten.

During the last quarter of the seventeenth century a new era of explorations was initiated by French adventurers who attempted to reach the Gulf coast from the north in order to establish there new colonies. In 1673 two French explorers, Louis Joliet and Father Marquette, descended the Mississippi River from Lake Michigan and voyaged south to the mouth of the Arkansas River.

In 1682 La Salle entered the Mississippi by way of the Illinois route, explored the river to its mouth, and in the name of France took possession of its entire drainage basin. Seeing great political and economic advantages in establishing a colony at the mouth of the Mississippi River, he obtained support of the French Government and in 1684 sailed from Europe with four ships, one of which was shortly captured by Spaniards. La Salle missed the mouth of the Mississippi River and landed farther west in Matagorda Bay, Texas, where he established his colony. Misfortunes, disease, and death so devastated the ranks of the colonists that in a few years only 45 survivors remained from several hundred who comprised the original party. In desperation, La Salle decided to reach Canada by land and during this journey was assassinated by his men.

One of the results of La Salle's exploration, which is of definite interest to the geography of the Gulf, is the sketch map of the location of his camp on the shores of Matagorda Bay with the soundings shown in feet. The reproduction of this map, in the form of a tracing from a photograph of the original, is given by Dunn (1917, p. 33).

Rumors of the French penetration in the land bordering the Gulf aroused the half-dormant rivalry between Spain and France and induced the Spanish Government to send several military expeditions with orders to destroy French colonies. As one of the official documents of that time stated, it was necessary to "desarraygar esta espina que se a yntroducido en el corazon del cuerpo de la America" which means to uproot the thorn that had been thrust into the heart of America (Dunn, p. 42).

In 1686 Martin de Echegaray, a naval captain of the presidio of St. Augustine, Florida, attempted to interest the Spanish Government in strengthening Spanish influence in the domain of Florida by transporting 50 Spanish families from the Canary Islands and 25 Indian families from Campeche. In support of his plan, Echegaray submitted a map, which is a good example of the defects of the geographical knowledge of that time, of the interior of the American continent. The Echegaray map shows the large "river Canada," or St. Lawrence River emptying into a lake from which two rivers lead southward to the Gulf of Mexico, both emptying into Espiritu Santu Bay (Mississippi River). Echegaray's scheme was not accepted, but the Spanish Government took other measures to counteract the French penetration into the new continent and to destroy La Salle's colony of which they were afraid. An interesting account of these attempts is given by Dunn (1917). It is sufficient to mention here that not less than four maritime expeditions were sent by the Spanish Government, and the whole Gulf of Mexico was examined with great diligence. One of the important results of this search for French colonies was the rediscovery of Pensacola Bay which the Spaniards decided to occupy. Admiral Pez was placed in command of an expedition organized for this purpose in 1693. One of his principal companions was Dr. Carlos de Siguenza y Gongora, professor of mathematics in the Royal University of Mexico and chief cosmographer of the kingdom. Siguenza kept a detailed journal of the journey in which he recorded his observations. The vessels of the expedition reached Pensacola Bay on St. Mary's

Day, August 14, 1693, and following their custom, the Spaniards immediately renamed it "Bahia de Santa María de Galve," the last name being added to the holy name of the Virgin in honor of the viceroy of the territory. Siguenza made a detailed survey of Pensacola Bay and described its configuration, depth, islands, and rivers. The expedition proceeded farther east and after some difficulty entered Mobile Bay, made soundings in the channel, and found that the depth was only 20 "palmas." As a result of Siguenza's observations strong recommendations were made to occupy Pensacola, but a final order for this action was not issued until 1698.

Rivalry among the western European powers in establishing a foothold on the shores of the Gulf of Mexico greatly enhanced the geographical knowledge of the region. As a military necessity the whole northern coast of the Gulf, with harbors, rivers, and lagoons, was surveyed; fairly accurate navigational charts were prepared; and information was accumulated regarding the prevailing winds and currents. In this way marked progress was attained in the cartography of the Gulf and adjacent coastal lands.

EIGHTEENTH CENTURY

At the beginning of the eighteenth century sailing vessels of European powers engaged in trade or in pursuit of military designs continued to traverse the waters of the Gulf in ever increasing numbers, but the era of ambitious expeditions and daring adventures, which in the past fired public enthusiasm, was over. As a matter of routine the ships made astronomical observations and determined the longitude and latitude of the places already known, surveyed the harbors and passes, made numerous soundings, and recorded the direction and velocities of winds and currents. These navigational data were eagerly sought by the cartographers to be incorporated in new maps, numbers of which appeared in various European countries and in Mexico. Examples given below, which illustrate this progress, have been selected from a large array of the cartographic material issued during this period.

French interest in the Mississippi River and the surrounding country is clearly expressed in the work of the famous French geographer, Guillaume Delisle (in the French publications the name is spelled "de L'Isle" and "Del'Isle") whose chart of Louisiana and of the course of the Mississippi was composed in 1719. The inscription reads that it was drawn after consulting many memoirs of Le Maire and others. The map shows the routes of De Soto and of other explorers and depicts the course of the principal rivers. The name Texas (Los Teijas) for the first time appears in cartography. According to Kohl (1857, No. 238), the Delisle map is "the mother and main source of all the later maps of the Mississippi and of the whole West of the United States."

The entrances to the Mississippi River, being of great importance to the French mariners, were surveyed with great persistency. Among the many persons who contributed to our knowledge of the physiography of the river, Lemoyne de Sérigny occupies a prominent position. In 1719 he participated in military operations in Florida and Louisiana and led a successful attack from the sea against Pensacola. His observations along the northern part of the Gulf coast are incorporated in a map drawn by an anonymous French cartographer and entitled "Carte de la côte de la Louisiane depuis l'Embouchure du Mississippi jusqu' à la Baie de St. Joseph, etc." The Library of Congress has a photographic reproduction of this document. The original is in Paris in Depôt de la Marine. Sérigny produced, also, a detailed map in colors of the approaches to Pensacola Bay. The notation on the body of the latter map contains reference to a strong surface current and the rise and fall of tides approximating 3 feet during a 24-hour period.

In connection with the construction of fortifications around the recently founded city of New Orleans, the French Government detailed many engineers to Louisiana. Among them Bernard de la Harpe distinguished himself by numerous observations which were incorporated in the de Beauvilliers map of 1720. The map shows many streams, mountains, towns, and Indian villages along the Gulf of Mexico and many islands off the coast of Yucatán. The chart of the Louisiana coast drawn about the same time (1719–20) by Devin was also made on the basis of the reports of De la Harpe and other French army officers. It shows many soundings and the positions of shallows and reefs in St. Louis Bay and adjacent waters.

The necessity of having accurate maps for safe

navigation along the coasts of America was fully recognized in England. Among the many charts published there during the first half of the eighteenth century that of Henry Popple, issued in 1733 on 20 sheets with an index, is of particular interest. This large chart, measuring 232 by 239 centimeters has the following title: "A Map of the British Empire in America with the French and Spanish Settlements adjacent thereto." A prospectus attached to the first impression contains a detailed description of the map. The Library of Congress has three impressions, one of which is imperfect.

About the middle of the eighteenth century the Spanish Government, feeling the need for more accurate information regarding the extent of its dominions in the New World, demanded by the royal decree of 1741 the submission by local authorities of detailed suveys of their administrative districts. Data thus obtained were summarized by Don José Antonio de Villaseñor y Sanchez, Auditor General of the Department of Quicksilver, who enjoyed a reputation as a "distinguished mathematician, accurate historian, and a good citizen" (Bancroft, 1883–86, v. 3, p. 510). The entire undertaking resulted in the map issued in 1746 under the title, "Icomismo hidroterro ó Mapa Geographico de la America Septentrional" (original in Arch. Gen. de Indias, Seville; copy in Library of Congress). In the same year the Spanish Government detailed Fernando Consag to explore the upper part of the Gulf coast. A reproduction of his map is given by Bancroft (1883–86, v. 1, p. 463).

Jacques Nicolas Bellin, an engineer of the French navy, was probably the most outstanding cartographer of the second half of the eighteenth century. In carrying out official orders of the French Government he made a detailed survey of the coast of Louisiana and of the course of the Mississippi River, drew a plan of Pensacola Bay (1742), published marine atlases and many maps (Bellin 1749, 1755, 1764). His map of the Gulf of Mexico and of the islands of America, issued in 1754 and published in volume 12 of Prévost's Histoire générale des voyages (1746–89, pp. 8–9), illustrates the state of geographical knowledge of that time. One can see from this map (fig. 6) that the configuration of the Gulf, especially along its west coast, is still incorrect, and the shape of the Florida Peninsula is far from being true. In this respect, as well as in the manner of drawing and the angularity of the coastal line, Bellin's map resembles the one prepared by his predecessor, Royal Cartographer D'Anville, in 1731 (fig. 7). Although the outlines of Florida are almost identical in the two maps, it is interesting to note that Bellin does not show such a fantastic array of bays and sounds as are indicated in the southernmost part of Florida by D'Anville.

One of the most notable documents of the second half of the eighteenth century is a map of the British and French dominions in North America published in London by John Mitchell in 1775 in accordance with the Act of Parliament (Mitchell 1755, 1757). The original of one of the earlier issues, identified by only one insert (Hudson Bay) instead of four in the later editions, can be found in the library of Harvard University. A copy of a French edition of 1756 is in the Library of Congress.

Mitchell's map was first used by American and British diplomats at the Paris peace conference of 1782–83 after the surrender of Cornwallis at Yorktown. Since that time it had been referred to and quoted as an authentic document in many boundary disputes between the United States and European countries.

The Harvard University copy has an interesting quotation from John Adams attached to the map which reads as follows: "We had before us . . . a variety of maps but it was the Mitchell's map upon which was marked out the whole boundary lines of the United States." The map shows only a small section of the northern part of the Gulf of Mexico between longitudes 83°4′ and 97° W. and latitudes 28°20′ and 30°20′ N. Tampa Bay is still called Baia del Espiritu Santo, and there are interesting notations regarding the depth of the water "20 feet water over the Bar of Pensacola the Chief Harbour hereabout" and the depth of "Y^{e} Missisipi" stated to be "18 feet water into Balise, 12 feet over the Bar, 45 feet within, 50, 60, and 100 afterwards."

In 1764–71 George Gauld ordered by the British Admiralty to make a survey of the coast of the provinces of West Florida and Louisiana, produced a map known as "Admiralty Chart." He also gave accounts of his surveys of Florida and sailing directions in the West Indies and Florida Keys (Gauld 1790, 1796). Several editions of Gauld's maps were issued in the United

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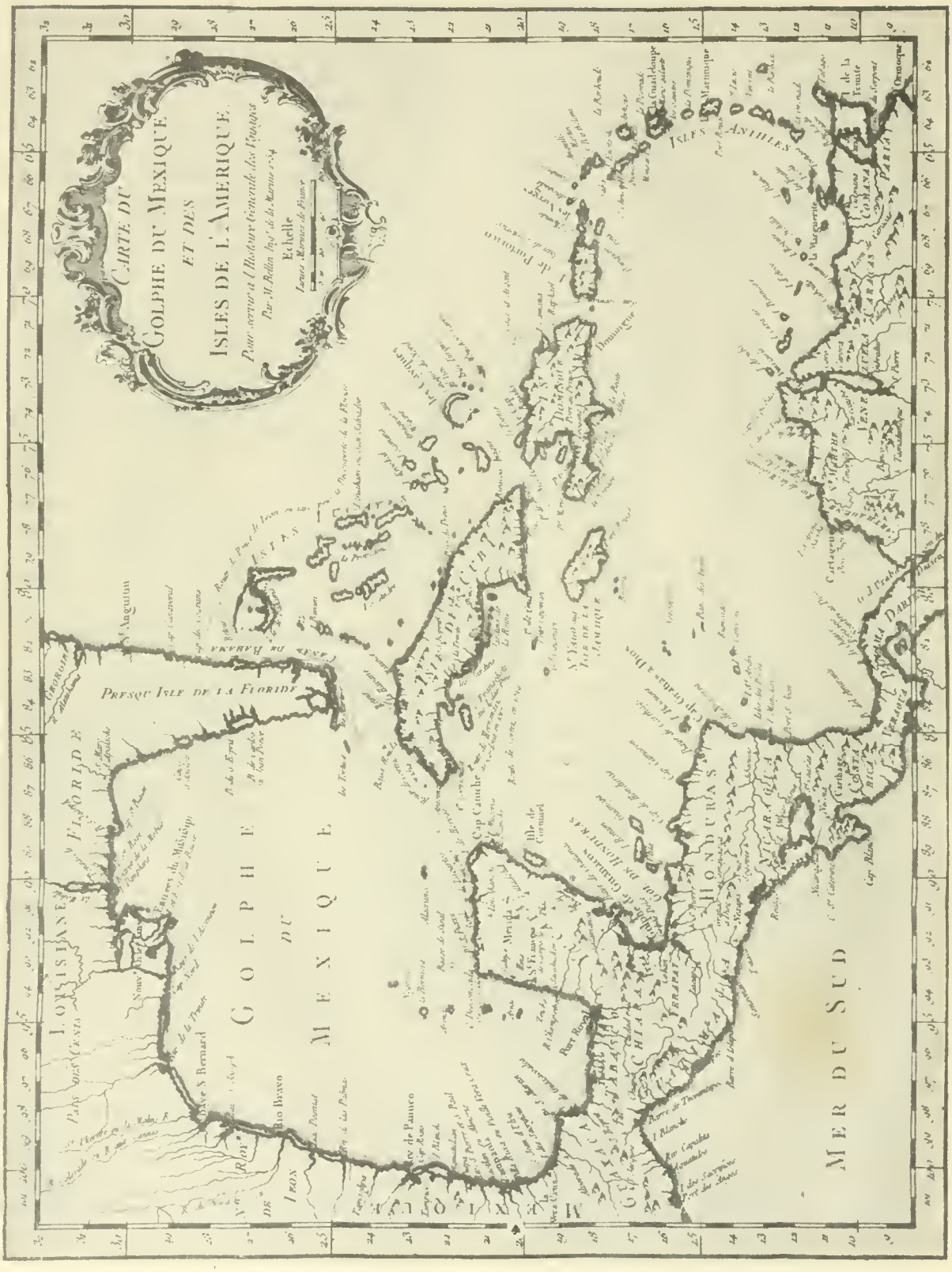

FIGURE 6.—French chart of the Gulf of Mexico and of the islands of America by Bellin, 1754.

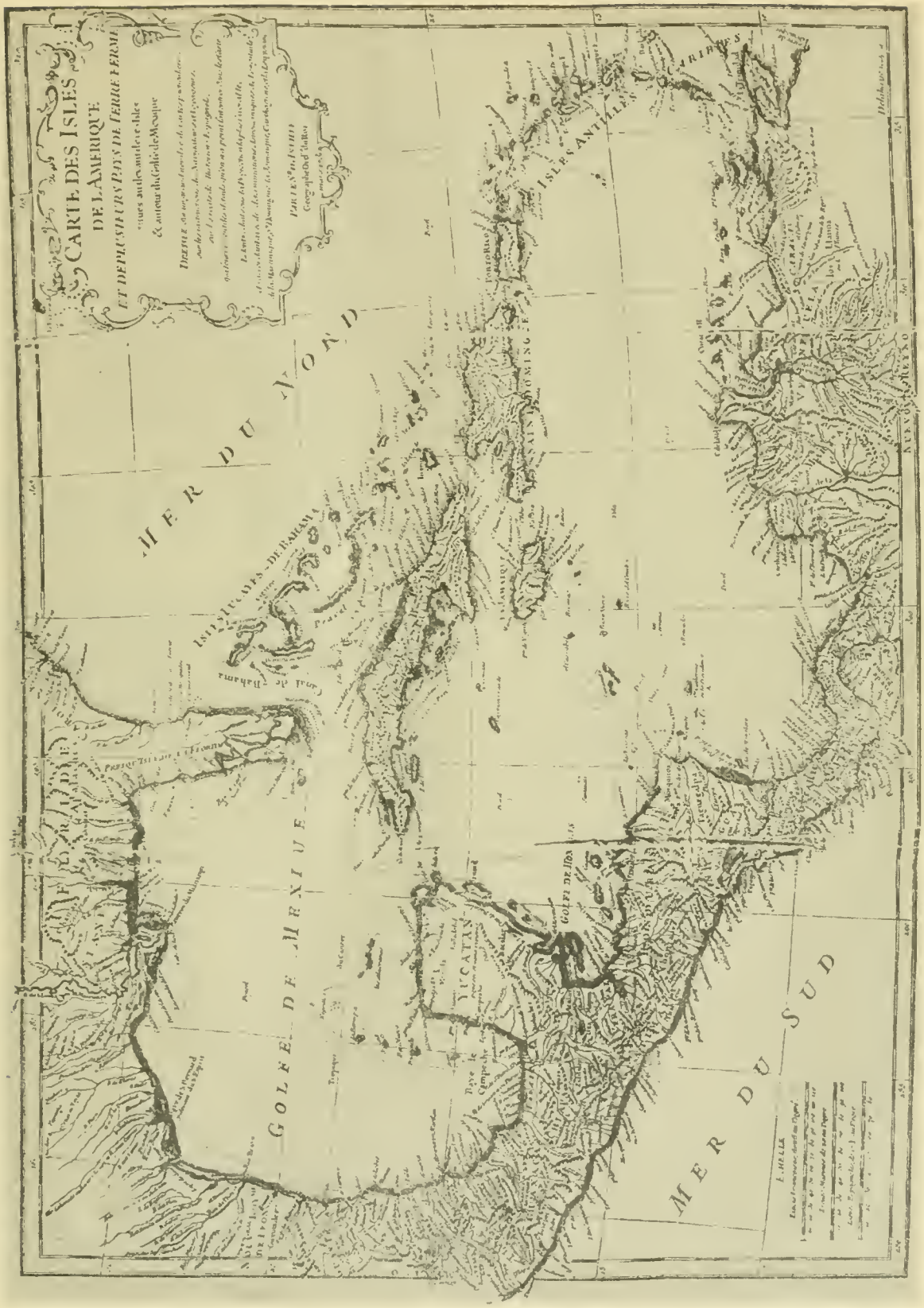

FIGURE 7.—French chart of the islands of America and adjacent countries by D'Anville, 1731.

States and in England and can be found in the Library of Congress.

In 1774 Captain Bernard Romans published a chart of the coast of East and West Florida to accompany his book on natural history (Romans 1776). The document is dedicated to the Marine Society of the City of New York; it is so rare that its existence was doubted by some bibliographers. The original is now in the Harvard University Library, and the map was referred to in Senate Document, 30th Congress, 1st Session, Report of Committee No. 242, August 12, 1848, to accompany Bill S. No. 338, relating to the Ever Glades. Romans' observations are of interest to biologists on account of the list of higher plants of Florida collected and identified by him and because of his remarks concerning the fisheries of Florida and Georgia. According to his statement, the principal fishes caught for trade and export were red drum (called in East Florida "bass" and in West Florida "carp"), pompano, sole, sea trout, and mullet. Oil was extracted from the livers of "nurses" (sic) and sharks, and glue was made from sea trout by drying them. The product was, using Romans' expression, "a perfect ichtyocalla."

Although no organized studies of the hydrography and oceanography of the Gulf were conducted during the eighteenth century, information received by the admiralties of the European countries from captains sailing the Gulf waters provided material for the corrections of the existing maps.

An interesting translation of a Spanish document was published about 1740 in London (Carranza 1740). The manuscript and the chart of the West Indies were given Carranza by a prisoner in Havana as a token of friendship. The book contains interesting data on tidal currents, description of shoals along the coasts of Yucatán and Florida, and depicts the channels that should be followed in navigation. Chapter 5 deals, in a rather detailed manner, with the currents and gives information on the variation of the compass which, as stated in the text, "is easterly, that is to say, in that part of it, among the shoals of Campeche it is 3°20′, and when you are out of soundings, 4°30′; in the middle of the bay 5½° to 6° and on the coast of La Vera Cruz, it amounts to 7°."

Incidental biological observations were occasionally reported by seafaring captains. Captain Uring (1726, new ed., 1928) mentions, for instance, many sea turtles his crew found on the shore when his ship was aground in Campeche Bay. He states that from June to August they lay eggs of which he counted as many as 150 in a litter. He found, also, in the same bay a large herd of "sea cows, or manatees, from 12 to 14 feet long and weighing from 800 to 1,000 pounds," about which he writes, "the flesh of it was as white as the finest veal. Their hides are cut into small strips to make whips which the poor slaves are well acquainted with all over West Indies." He makes numerous references to sand flies and troublesome "muchetos" infesting the woods. No biological studies were undertaken, however, during this period, and no attempts were made to obtain a representative collection of plants and animals of the Gulf.

FROM THE BEGINNING OF THE NINETEENTH CENTURY TO THE PRESENT TIME

At the beginning of the nineteenth century the geographical knowledge of the Gulf of Mexico made marked progress. As can be judged from the charts of that period the configuration of shoreline including the coasts of Florida and the Yucatán Peninsula appeared to be almost correctly outlined; many shoals and banks were shown with numerous soundings and notations regarding the character of bottom together with other hydrographical data. The Spanish map of Don Juan Langára, issued in 1799 and revised in 1805, is a good example of the best type of cartographic material available at this time (issues of this map are in the Library of Congress and in the American Geographical Society).

By the middle of the nineteenth century gross inaccuracies apparent in the older issues were almost eliminated as can be seen by examining Laurie's map (fig. 8) published in 1856 in London or a chart which appeared in a French manual for navigation in the Caribbean Sea and the Gulf (Kerhallet 1853). The latter map shows a general picture of the movement of surface waters, depicts the ingress of the Antillean Current, and indicates the existence of a large eddy in the central part of the Gulf (fig. 9).

In the United States the act of Congress of February 10, 1807, inaugurated a new era of ma-

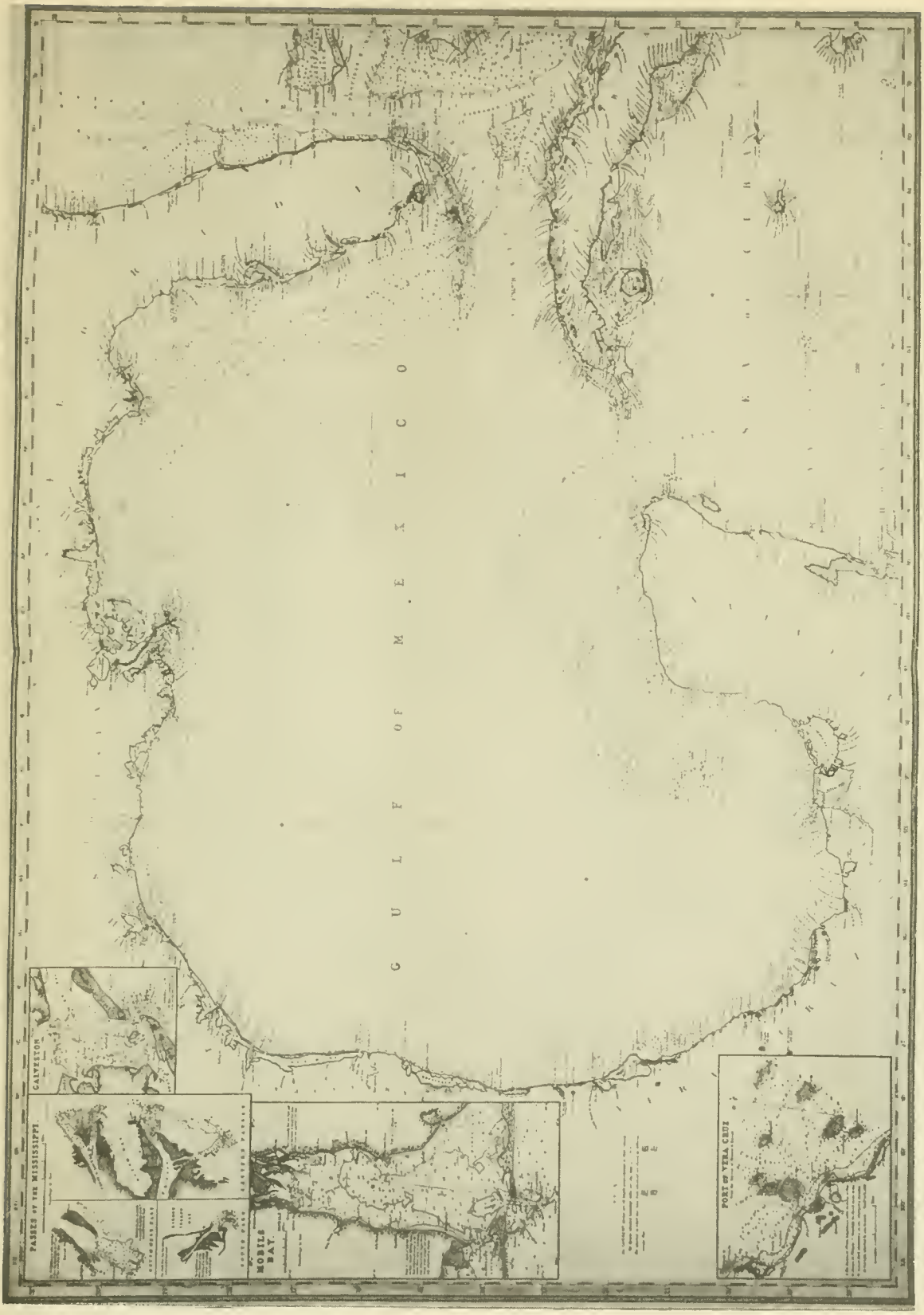

FIGURE 8.—English map of the Gulf of Mexico by Laurie, 1856.

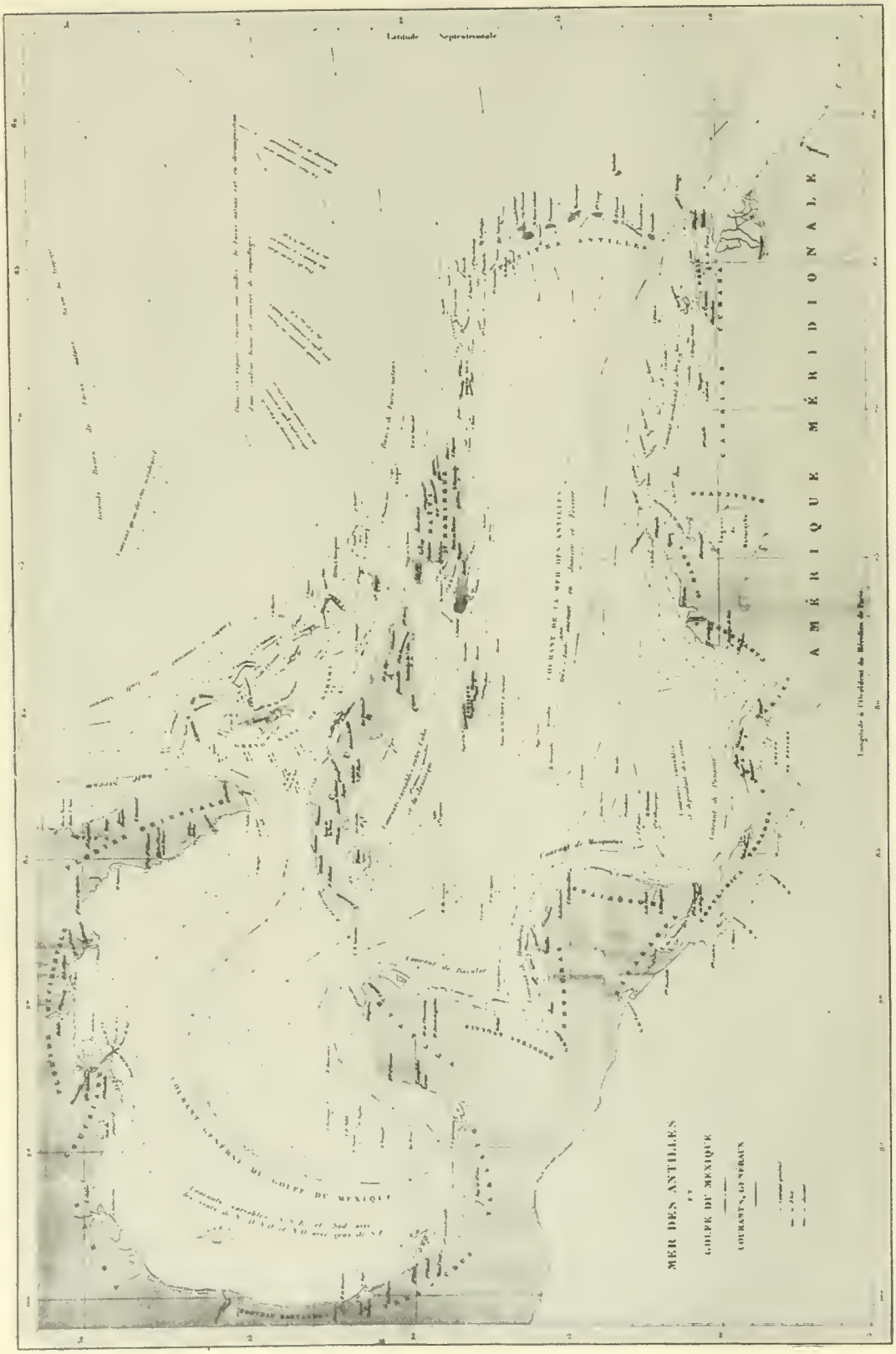

FIGURE 9.—French map showing circulation of water, from the Manual of Navigation, by De Kerhallet, 1853.

rine explorations by authorizing the President to "cause a survey of the coast of the United States and to employ proper persons in accomplishing the purpose prescribed in the act," for which a sum not exceeding $50,000 was appropriated. From 1816 to 1843 the reports of the Superintendent of the United States Coast Survey, made in compliance with this act, contained no references to the work in the Gulf of Mexico. Some explorations in the Gulf were conducted, however, by the United States Navy. In 1839 the U. S. S. *Vandalia*, under the command of Uriah B. Levy, was engaged, from February 4 to August 3, in the hydrographic exploration between Galveston and the southwestern pass of the Mississippi River.[3]

The reconnaissance survey of the Gulf coast was commenced by the United States Coast Survey in January 1845 (Report of the Superintendent for the year ending November 1846), and since that time the work of the organization, renamed in 1878 United States Coast and Geodetic Survey, is being continued at the present time. A large number of hydrographic and topographic charts issued during this time show the high degree of perfection achieved by this agency during more than a century of continuous work. The years of different surveys made in various sections of the Gulf can be found in the Hydrographic Index Charts, Nos. 80–91, and Topographic Index Charts, Nos. 20–32, issued by the United States Coast and Geodetic Survey.

The main features of the Gulf—the configuration of its bottom and the circulation of water and its emergence as the Gulf Stream—were the objects of many investigations. The exploration of the Gulf Stream was commenced in 1844 by Davis (Report of the Superintendent, U. S. Coast Survey, year ending November 1846) and was continued by Bache in 1846, who inaugurated a series of deep-sea investigations of the physical problems connected with the Gulf Stream (Bache 1852, 1859). This work was expanded by his successors in the United States Coast Survey, Benjamin Price, Carlile P. Patterson, and Julius E. Hilgard. The results of the Gulf Stream explorations, including observations of distribution of water temperatures in the Florida Channel and Straits, were discussed by Bache in several articles (Bache 1854, 1860).

In 1850, at the request of the United States Coast Survey, Professor Louis Agassiz undertook an extended biological survey of Florida reefs and obtained valuable information concerning the topography of Florida, the mode of formation of reefs by cementation, and the origin of the Florida Keys (L. Agassiz 1880).

Occasional references to bottom animals of the Gulf are found in French publications of Folin and Perier (1867–72), in which are described several new species of mollusks and ostracods from the bottom deposits collected near Veracruz and in Laguna de Términos.

Maury's (1858) classical book on the physical geography of the sea contains no specific reference to the Gulf of Mexico except a brief note concerning the corrosive action of Gulf waters, which were observed to be more destructive to copper sheeting of ships than the water from any other part of the world.

Systematic deep-sea explorations carried out in 1867 and 1868 by Pourtalès and Mitchel on the United States Coast Survey ships *Corwin* and *Bibb* consisted in dredging between Florida and Cuba, at some places at a depth of 850 fathoms. Many new types discovered in these collections and the finding of species of corals and echinoderms which were considered related to an antique fauna of the Cretaceous period, proved that a study of bottom organisms thriving along the course of the Gulf Stream is of great scientific interest (Pourtalès 1867; L. Agassiz 1852; A. Agassiz 1888, v. 1, p. 49; Peirce and Patterson 1881).

Explorations along the west coast of Florida undertaken in 1872 by Commander Howell were continued in 1875–78 in other parts of the Gulf under the direction of Lieutenant Commander Sigsbee aboard the United States Coast Survey steamer *Blake*. In the following years the operations were extended, under the command of Commander Bartlett, through the Caribbean Sea and the Straits of Florida. Alexander Agassiz, in charge of dredging operations of the *Blake* expedition, made a geological study of Florida reefs which had already attracted the attention of his father, Louis Agassiz, Le Conte, and Hunt (A. Agassiz 1888, v. 1, pp. 52–92).[4]

[3] Copy of the chart of the cruise of the *Vandalia* is in the Library of the American Geographical Society of New York.

[4] The geology of the Gulf of Mexico is discussed in an article by S. A. Lynch in this book, pp. 67–86.

Three cruises of the *Blake*, from 1877 to 1880, represent an outstanding event in the history of scientific explorations of the Gulf of Mexico. The expeditions obtained a wealth of information regarding the oceanography and biology of the Gulf, and the two volumes describing the work of the *Blake* written by A. Agassiz (1888) until the present day remain an important source of reference concerning the bottom fauna, the structure and origin of coral reefs, and the distribution of invertebrates and fishes at depths extending to 2,000 fathoms.

Collections obtained by the *Blake* served as material for many important publications on corals, antipatharians, crinoids, and Crustacea (Pourtalès 1870, 1880); echinoderms (A. Agassiz 1863, 1869, 1878, 1883); hydroids (Clarke 1879); annelids (Ehlers 1879); mollusks (Dall 1880, 1886, 1889), and many others. Numerous papers dealing with various taxonomic groups gathered by the expeditions can be found in the first 19 volumes of the Bulletin of the Museum of Comparative Zoology at Harvard College. A discussion of the deep-water fauna of the Gulf Stream was given by Pourtalès (1863–69).

The establishment, in 1871, of the United States Commission of Fish and Fisheries marked the beginning of the study of the important coastal and marine fisheries of the Gulf. With the building of the 1,000-ton steamer *Albatross* in 1883, the first Commissioner of Fisheries, Spencer F. Baird, initiated worldwide explorations of the sea fisheries. At the time of her completion, the *Albatross* was the best equipped dredger for deep-sea work in existence. One of her first details was to explore the bottoms of the Gulf of Mexico. The instructions given in 1883 by Spencer F. Baird to the commanding officer, Lieutenant Commander Z. L. Tanner, read in part as follows: "In returning (from the Caribbean) by way of Cape San Antonio it will be well to make a run into the Gulf of Mexico and spend a short time in making soundings and dredging therein, for the purpose of obtaining a general idea of the natural history and the fisheries of the Gulf, preliminary to a more lengthened visit to be made hereafter" (Tanner 1886). The instructions specified that in addition to the purely physical work, soundings, temperature, and observation of currents, the *Albatross* should secure "a fair representation of the shore fauna of the Caribbean Sea and its surroundings including shallow water, to collect parasites of the larger fish, birds, reptiles, freshwater fish, and the various species of mammals as well as to obtain aboriginal relics in the way of articles of stone, pottery, etc." Large collections made by the *Albatross* and deposited in the Smithsonian Institution testify that the instructions were faithfully carried out.

During the first visit to the Gulf in 1884 the *Albatross* explored the bottoms around the western tip of Cuba (fig. 10, open squares) but returning in the following year made more detailed explorations around Cozumel Island, along the eastern edge of Campeche Bank, on red-snapper banks off Cape San Blas in the northeastern part of the Gulf, and occupied a few stations along the west coast of Florida and at Key West (fig. 10, black double circles).

A brief but interesting account of the history of the *Albatross* is given by Hedgpeth (1945, 1947).

Simultaneously with the oceanographical studies the United States Fish Commission conducted an exploration of the fishery resources of the Gulf of Mexico. Accounts of this work with reference to red snappers, shore seine fishery, oysters, and sponges are given by Stearns (1884, 1887), Collins (1887), and Stearns and Jordan (1887).

In 1880 the United States Commission of Fish and Fisheries built a steamer, *Fish Hawk*, for the purpose of assisting in fish-hatching operations and conducting surveys of fishing grounds. From November 1895 to 1896, under the command of Lieutenant Franklin Swift, the *Fish Hawk* surveyed oyster regions of St. Vincent Sound, Apalachicola Bay, and St. George Sound, Fla. (Swift, 1897), the work which 20 years later was repeated with the same ship by Danglade (1917). In 1898 the *Fish Hawk* was used by the United States Coast and Geodetic Survey in hydrographic investigations of the inshore waters of Alabama. In 1901 and 1902 the ship was engaged in sponge investigations along the west coast of Florida. The exploration in 1901 covered the grounds between Anclote Anchorage, St. Marks, and Tampa Bay. In the following year the operations extended along the western coast of Florida, to the depth of 10 fathoms, from Cedar Keys to Key West. In 1905 the *Fish Hawk* was detailed to survey the oyster bottoms and make hydrographic investigations in Matagorda Bay, Tex. (Moore 1907), in 1911 made a similar investiga-

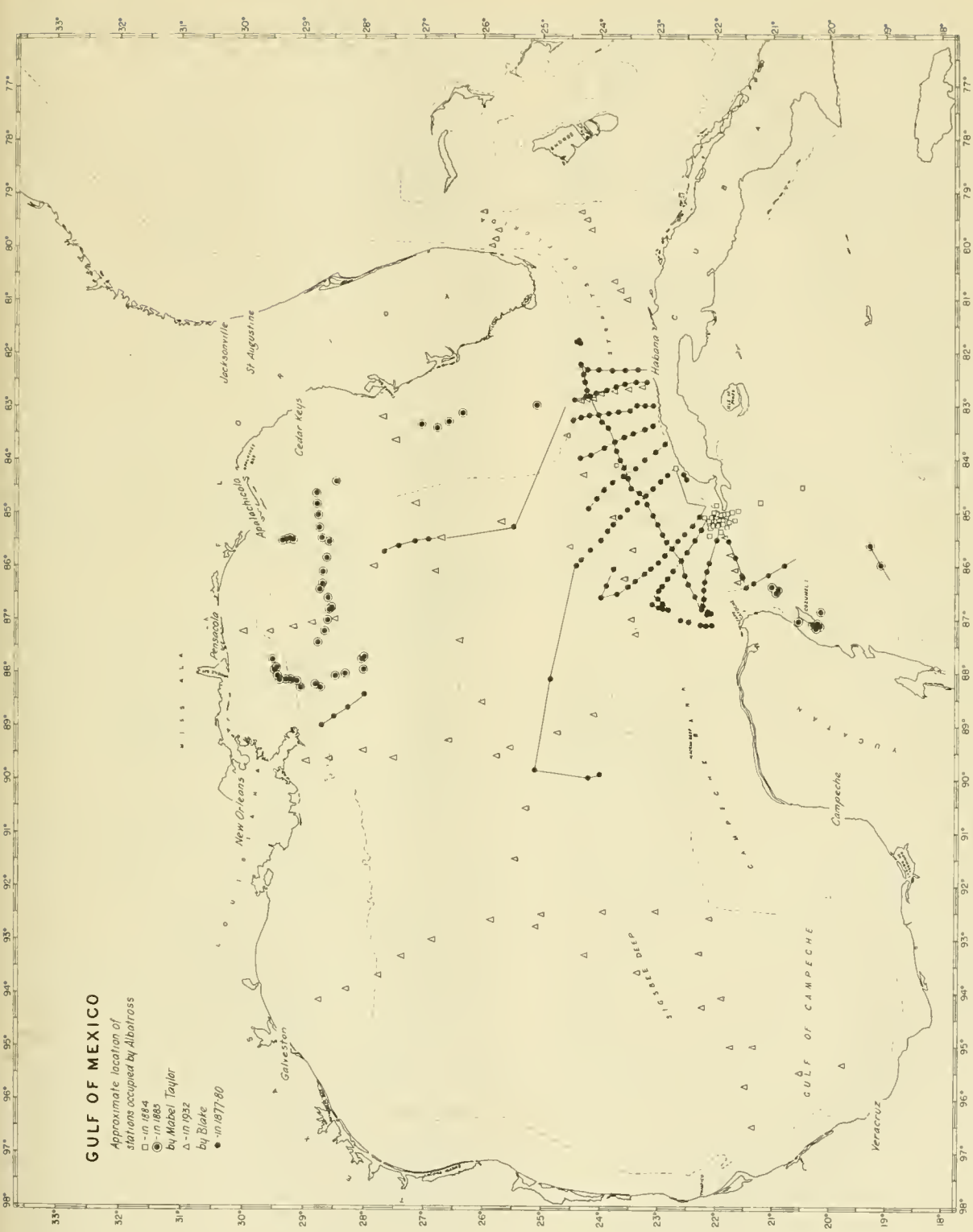

FIGURE 10.—Approximate location of stations occupied by the *Blake*, 1877–80, (black circles); the *Albatross*, 1884, (open squares), 1885, (black double circles); and the *Mabel Taylor*, 1932, (triangles).

tion in Mississippi Sound (Moore 1913a, 1913b), and in 1913 was used as the base for a survey of oyster bottoms in Lavaca Bay, Texas (Moore and Danglade 1915). The completion of the latter investigation by Moore marked the ending of the *Fish Hawk* activities in the Gulf.

In 1917 the research ship *Grampus* of the United States Bureau of Fisheries cruised over the continental shelf from Key West to Aransas Pass in a study of shrimp and fishery grounds (U. S. Bureau of Fisheries, 1919).

The results of systematic hydrographic work conducted by the United States Coast and Geodetic Survey and the Hydrographic Office of the United States Navy with the additional data accumulated by other explorations served as a source of material for a general discussion of the physiography of the Gulf. Forshey (1878) attempted to describe the configuration of the bottom of the Gulf, stressing particularly the deposition of sediments brought in by the Mississippi River which he believed eventually will fill up the Gulf. Lindenkohl (1896) summarized temperature and salinity data taken primarily from the reports of the United States Coast and Geodetic Survey.

In order to obtain basic data on physical oceanography of the Gulf a plan was adopted in July 1905 by the Hydrographic Office of the United States Navy to supply all vessels crossing the Gulf with a form for daily use in giving ship's position, direction and force of the wind, direction and force of the current, and temperature and color of the water. The reports of hundreds of observers extending over a period of years, when plotted on the monthly charts, agreed remarkably. The data were summarized by Soley (1914) on a chart entitled, The Gulf Stream in the Gulf of Mexico (see Pilot Chart of the North Atlantic Ocean for June 1914), reproduced in figure 11. Soley's chart shows the basin of tidal equilibrium (Sigsbee Deep) more than 2,000 fathoms deep in the western part of the Gulf, the direction of the main current, and the Gul' Stream which comes from the North and South Equatorial Current in the Yucatán Channel. The Northwestern Branch of the Current leaves the main stream at the northeastern corner of Campeche Bank, while the Eastern Branch turns eastward from the Yucatán Channel. The chart shows, also, the two countercurrents, the Cuban and the Western, and the position of the Central Sea, a circular body of dead water about 80 miles in diameter. From the time of the first publication of Soley's chart basic information given in it is being incorporated in monthly pilot charts regularly issued by the Hydrographic Office of the United States Navy with the additional data supplied by ships and provided by the United States Weather Bureau of the Department of Commerce (formerly a part of the U. S. Dept. of Agriculture).

In January–March 1914 Bigelow (1915), working on board the United States Coast and Geodetic Survey steamer *Bache*, made observations in the Straits of Florida studying vertical distribution of temperature and salinity from the surface to the depth of 1,800 meters along the profiles drawn across the Straits from Key West to Havana, from Cape Florida to Gun Bay, and from Jupiter Inlet to the northern end of Little Bahamas Bank. He noticed the banking up of cold water against Florida as a result of upwelling from deep layers on the left side of the channel and concluded that the cold, comparatively fresh water next to Florida is largely true abyssal water from the Gulf of Mexico.

In 1926 the oyster bottoms in the bays along the coast of Texas were surveyed by Galtsoff (1931) with special emphasis on salinity distribution in these bodies of water. From 1936 to 1939 a detailed work on the hydrography of Texas tidal waters was carried out by Collier (Collier and Hedgpeth 1950).

The natural history of redfish and other sciaenids on the Texas coast was studied by Pearson (1929) who pointed out the scientific importance in a study of the biological relationship between the Gulf and its inland waters.

Marked advance in the knowledge of the hydrography of the Gulf was made in 1932 by the Yale Oceanographic Expedition of the *Mabel Taylor* sponsored by the Bingham Oceanographic Foundation. One of the chief problems of the investigation, formulated by the leader of the expedition, Parr (1935), was to study "the relationship between the waters in the region of the Straits (*i. e.*, the area southward between the Yucatán Channel and the Straits of Florida) and in the Gulf of Mexico proper." Such a study became highly desirable in view of Nielsen's (1925) objections against the purely two-dimensional picture of surface movements of water in the Gulf

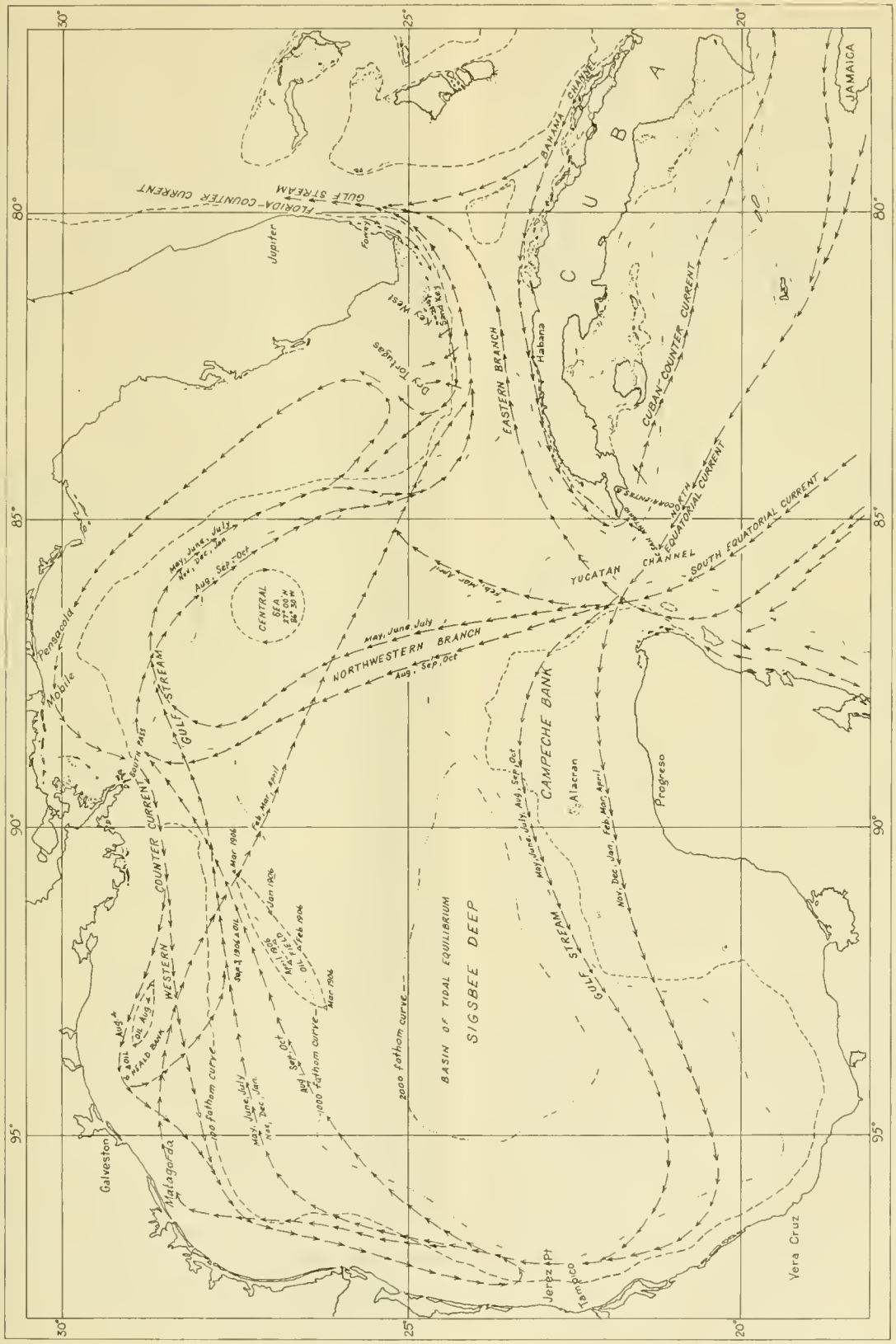

FIGURE 11.—Gulf Stream in the Gulf of Mexico shown by Soley's chart, 1914. The currents as they exist during the different seasons.

of Mexico given in Soley's chart. The expedition occupied 87 stations (fig. 10, triangles) at which temperature and salinity of water were recorded at different levels from surface to a depth of 3,000 meters (1,640 fathoms).[5]

In 1934 the *Atlantis* of the Woods Hole Oceanographic Institution occupied, from January to March, a series of hydrographic stations in Yucatán Channel and the Straits of Florida, and in January to May 1937, jointly with the Bingham Oceanographic Foundation, made observations in the Caribbean Sea and Gulf of Mexico (Parr 1937a, 1937b). During the cruise of 1947, sponsored jointly by the Woods Hole Oceanographic Institution and the Geological Society of America, the *Atlantis* occupied 551 stations in the western part of the Gulf between Sigsbee Deep and the coasts of Louisiana and Texas. In 1951 observations were made by this ship at 240 stations. As a result of this work, combined with the data obtained by the United States Coast and Geodetic Survey, a very detailed map of submarine topography on the northwest quarter of the Gulf was issued by the Institution in 1951.

In 1951 the Fish and Wildlife Service of the United States Department of the Interior initiated a comprehensive research in oceanography and fishery resources of the Gulf of Mexico. This work is carried on by the U. S. S. *Alaska* and the U. S. S. *Oregon*, the latter ship being primarily concerned with the explorations of new fishing grounds. Material dredged by the *Oregon* and deposited in the U. S. National Museum in Washington proved to be of exceeding interest to zoologists, for it comprised many rare species which heretofore were represented only by isolated specimens.

A steady growth of interest in marine biology in the United States during the last half century is reflected in an increase in the number of laboratories or stations devoted to marine biological research in general, or to a study of specific problems of utilization and management of fishery resources. One of the earliest institutions of that type in the Gulf was the Gulf Biologic Station established in 1902 by the State of Louisiana at the mouth of Calcasieu Pass in Cameron, La. In 1910, by an act of the General Assembly, the Gulf station was merged with the State Conservation Commission, and about 2 years later the property consisting of 10 acres of land and the building in which the laboratories were located reverted to the original donor, Judge Henry, and the operation of the laboratory ceased. During its brief existence the Gulf Biologic Station was concerned primarily with the biology and cultivation of oysters, scallops, and clams in Louisiana waters and in studying the distribution and biology of local marine and brackish-water plants and animals. The contributions of the laboratory were published in 15 issues of the Bulletin of the Gulf Biologic Station issued from 1902 to 1910 and in 3 small biennial reports of the director dated 1906, 1908, and 1910.[6] Brief data regarding the founding of this station and its policy are given by Foote (1942).

In June 1904, the Carnegie Institution of Washington, D. C., established a marine laboratory at Loggerhead Key, Dry Tortugas, 68 miles west of Key West, Fla. The site was chosen because of the purity of the ocean water surrounding the group of seven, small, sandy islands, the proximity of the Gulf Stream with its abundant life, the presence of rich coral reefs in Florida, and the absence of local fisheries which could have affected the undisturbed life of the sea. Despite adverse conditions due to the difficulties of regular communication with the mainland, hurricanes which frequently swept the Keys, and the short season of its operation (restricted to 3 summer months), the station was very productive in scientific research. Its work inaugurated and conducted under the inspiring directorship of the late Dr. Alfred G. Mayer, covered a very broad field of research in marine biology and general physiology. The 33 volumes of the Papers from Tortugas Laboratory contain many fundamental works dealing with a great variety of problems such as biology of coral reefs by Mayer, the physiology of Valonia cells by Osterhout, the metamorphosis of ascidian larvae by Caswell Grave, observations on color, habits, and local distribution of the fishes of Tortugas by W. H. Longley, ecology and geologic role of mangroves by H. J. Davis. Many other papers of permanent scientific value came from the institution, which more than any other laboratory contributed to our knowledge of the marine life of the Gulf.

[5] For the discussion of Parr's work see article by D. F. Leipper, Physical Oceanography of the Gulf of Mexico in this book, pp. 119-137.

[6] I am grateful to Joel W. Hedgpeth for supplying the data regarding the Gulf Biologic Station.

American scientists interested in marine research were grieved to learn from the report of the director of the Carnegie Institution for 1939 of the discontinuance of the laboratory due to the "relatively high cost of its maintenance." At the time of this action the Laboratory was receiving a modest annual grant of $12,000 which constituted about 0.8 percent of the total budget of the Carnegie Institution of Washington for that year.

Brief mention should be made of the attempt of the United States Bureau of Fisheries to establish a fishery laboratory at Key West in 1917. Owing to the lack of funds for salaries and equipment the station never became functional and was abandoned in 1928.

A small laboratory is maintained by Louisiana State University on Grand Isle. The laboratory is used every summer from June to July for teaching. Despite modest equipment and lack of modern research facilities a number of valuable scientific papers resulted from its operations which have enhanced our knowledge of the Gulf fauna.

From 1935 to 1937 the United States Bureau of Fisheries maintained a temporary laboratory at Indian Pass in Apalachicola Bay, Florida, for the purpose of studying the biology of the oyster leech (*Stylochus inimicus*) and other enemies of the oyster. Upon completion of this work (Pearse and Wharton 1938) the laboratory was abandoned in 1937 and the equipment transferred to the fisheries laboratory near Pensacola, Fla. The latter laboratory, established in 1937 primarily for shellfish research, is located on a small island in Santa Rosa Sound about 7 miles from Pensacola. The laboratory, with several auxiliary buildings, occupies the site of the abandoned quarantine station. It is equipped with running sea water and outdoor cement tanks for experiments on shellfish. The current work consists in ecological and biological research on oysters in Florida, Alabama, Mississippi, and Louisiana waters.

The Marine Laboratory of the University of Miami was established in 1942 at Coral Gables, Fla., for research and teaching in oceanography, marine biology, conservation, and management of fishery resources. Its operations extend over the waters of the West Indies and the Gulf of Mexico. The laboratory maintains a station at Apalachicola for oyster studies and, as circumstances require, establishes temporary headquarters along the west coast of Florida. Principal research projects, some of which are sponsored by the United States Navy, deal with the circulation of water in the Gulf (Smith, et al., 1951), seasonal changes in the composition of plankton of Biscayne Bay and adjacent oceanic waters, red tide, sponge disease and sponge culture, physiology of fouling organisms, and many others. Several of the articles by the members of the laboratory staff appeared in the newly established Bulletin of Marine Science of the Gulf and Caribbean and in the Proceedings of the Gulf and Caribbean Fisheries Institute founded by the laboratory. The Gulf and Caribbean Fisheries Institute represents an effort to integrate the work of oceanographers, biologists, economists, fishermen, and administrators. It seems appropriate to point out here that the idea of preparing a digest of the existing literature on the biology and oceanography of the Gulf of Mexico originated at the Second Annual Session of the Institute and has materialized through the efforts of several members of this organization (Walford 1950).

Several other institutions devoted primarily to the study of Gulf problems, were established in recent years. The Institute of Marine Science of the University of Texas in Port Aransas was founded in 1948 with a grant from the General Education Board and with funds provided by the Texas Agricultural and Mechanical Research Foundation. The Texas Game, Fish, and Oyster Commission established, in 1949, a marine laboratory at Rockport, Tex. The Fish and Wildlife Service of the United States Department of the Interior has maintained, since 1949, a temporary laboratory for red-tide studies at Sarasota, Fla., and in 1950 established headquarters with laboratory facilities at Galveston, Tex., for the conduct of oceanographical and biological studies of the Gulf. The Oceanographic Institute of Florida State University was established in 1949 with two seaside stations, one at Alligator Harbor and another at the mouth of the St. Johns River about 12 miles east of Jacksonville at Mayport, Fla., on the Atlantic coast. Research facilities of these stations, engaged primarily in teaching, are limited.

Since 1947 the State of Mississippi has maintained the Gulf Coast Research Laboratory at Ocean Springs, Miss., for instruction in zoology and botany.

Recent oil-development activities in the coastal

area of the Gulf provided an opportunity to make continuous observations from fixed platforms erected several miles off shore. Analyzing these records, Geyer (1950) discovered that the salinity of water of the Louisiana coast at a distance from 5 to 6 miles from the shore undergoes seasonal variations ranging from 15 to 35 parts per thousand at 10 feet below the surface. Extensive investigations of the hydrography of the inshore waters and the effect of crude oil and brine on aquatic life have been recently sponsored by the oil companies. Unfortunately, the results of these studies are not available to the public.

The outlook for scientific investigations of Gulf problems appears to be bright. There are at present many laboratory and field facilities available at various scientific institutions located along the Gulf coast. Furthermore, Federal and State organizations show great interest in the research problems and are in a position to conduct or sponsor various oceanographic and biological projects. It is therefore reasonable to expect that the progress in our knowledge of the Gulf of Mexico will be rapid and productive.

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CHAPTER II GEOLOGY

SHORELINES AND COASTS OF THE GULF OF MEXICO [1]

By W. ARMSTRONG PRICE,[2] *Agricultural and Mechanical College of Texas*

INTRODUCTION

The scientific study of shorelines is inextricably involved with that of the hinterland, the coastal zones, the adjacent inshore waters and the climate. This linkage brings together regional geology, geomorphology, sedimentation, oceanography of the inshore zone, meteorology, climatology, biology, chemistry, late geologic history and the ecology of some marine and coastal organisms. As the study of shorelines and their classification is in somewhat incomplete and controversial condition today, it is necessary to give a brief review of the subject before discussing the shoreline of a particular region, such as the Gulf of Mexico, where there are new types and where we have previously had few over-all geological oceanographic conceptions to guide us.

STATUS OF STUDIES OF COASTS AND SHORELINES

The geological study of shorelines and coasts has been intermittently developed by numerous geologists and geographers. The principal discussions of costal geomorphology that are readily available are Johnson's (1919) detailed treatise on shoreline development and his study of the New England-Acadian shoreline (1925), Shepard's (1937a, 1948) revision of Johnson's shoreline classification, Steers' (1946, 1952) analytical description and history of the shoreline of England, Wales, and Scotland, and Russell's (1940) study of the development of variations in deltaic shorelines in Louisiana. McCurdy's (1947) discussion of criteria for the delineation of shorelines from air photographs yields critical details of some types not found elsewhere. Fleming and Elliott (1950) have made a beginning of an over-all quantitative and qualitative oceanographic approach to the study of shorelines which is here revised, enlarged and treated in greater detail, in some of its aspects, for the Gulf of Mexico. Some of the oceanographic data treated by these workers have not been considered here.

Among the greatest present needs in geomorphic coastal studies are a critical analysis and description of the coastal plain shoreline and regional studies combining the geomorphic and oceanographic approaches. The research on which this paper is primarily based was a comprehensive survey of the shorelines of the Gulf from existing data, including results of the writer's 20-year study of the northwestern Gulf Coast. The survey was made by the writer in 1951–1953.[3] It has revealed a number of new types and relationships not yet critically discussed in publication. Because of this situation, the writer is handicapped in attempting a discussion of the coasts of the Gulf of Mexico within as condensed a scope as that of the present paper.

The application of quantitative oceanographic science to the analysis of the development of shorelines is being slowly accomplished through the work of numerous scientists and engineers by isolated studies of beaches, cliffs, deltas and estuaries, but has only lately been attempted for whole regions. In the writer's current research, an attempt is being made to apply a quantitative regional approach to the study of the influence of oceanographic processes on shorelines and the associated coastal and shallow-water bottom conditions. Some of the results of this work are reflected in this paper.

SHORELINE CLASSIFICATION

Eduard Suess (1888) showed that regional or continental shorelines might be classed as concordant or discordant with the grain (dominant trend) of the geologic structures of a coastal region, but King (1942, p. 99) cautioned that marine activities subsequent to the drowning of a coast or the formation of its folds and faults may have

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[3] Contains no references to the work of others after March 1, 1953.

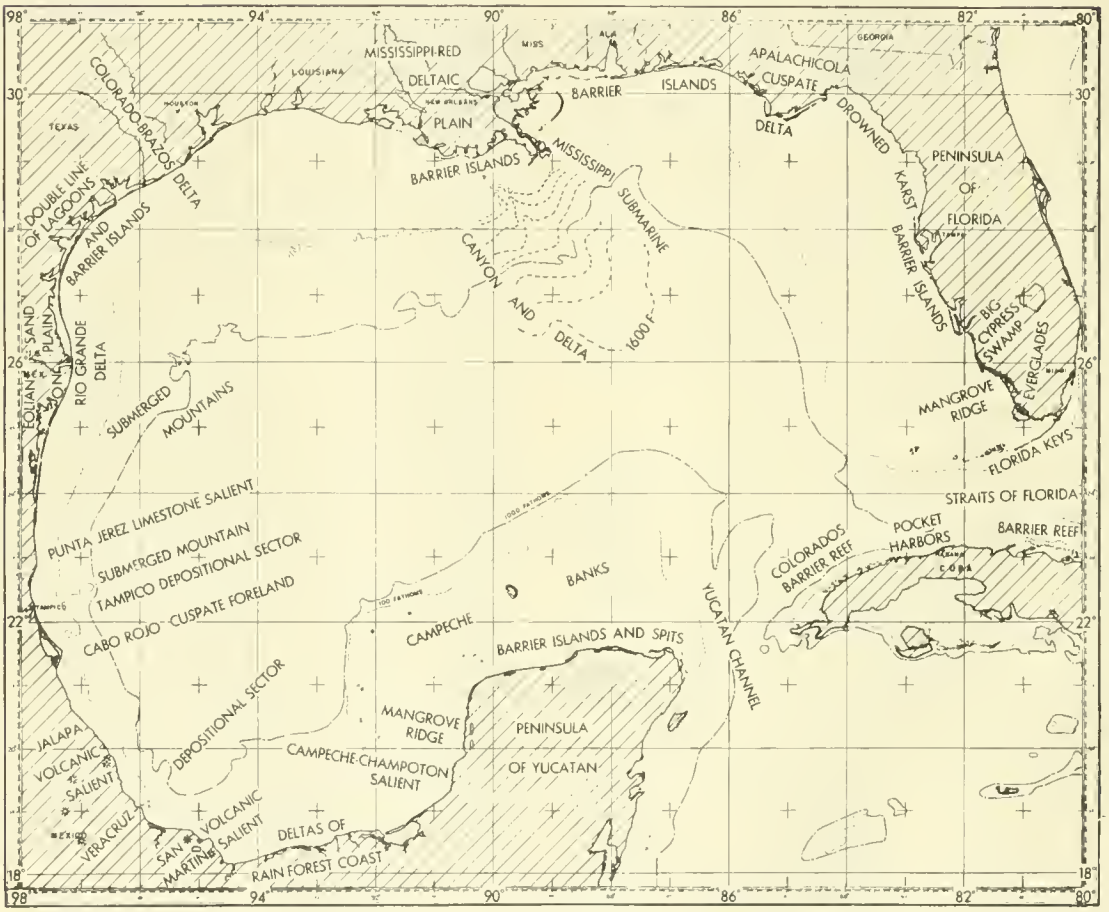

FIGURE 12.—Shorelines of Gulf of Mexico, showing locations of major geographic features. (Contour lines off the Mississippi delta are drawn at 200-fathom intervals.)

altered the shoreline so that it may no longer conform to a simple structural classification. Johnson (1919) assembled and extended previous ideas of coastal development and classification to produce a detailed genetic-geomorphic system that has since been followed by most writers. However, it seems not to have been applied by its users to the detailed mapping of the coasts of a large, diversified region such as the Gulf of Mexico, although Johnson (1925) applied it to the drowned and largely discordant shoreline of the New England-Acadian region of northeastern North America.

Shepard (1937a, 1948) modified and extended Johnson's system, giving a tabulation in which shoreline and coastal types then described were inserted. His major divisions differ from Johnson's and seem not to have been accepted by all of Johnson's followers, although the scarcity of papers on the classification of shorelines indicates that this may be due to inertia rather than to a working appraisal of the usefulness of Shepard's revised system. Johnson's text is out of print and has not been supplemented by a similarly detailed work.

Regional variations in the known physical oceanographic conditions in the "inshore" zone[4] of the coasts of the United States and Mexico were discussed by R. H. Fleming and F. E. Elliott (1950) in lectures. They regarded the scarcity of such information too great for elaboration of their method at that time. It, however, classifies coastal sectors into glacial, alluvial, young orogenic and biogenous types, with erosional and depositional sub-types for the first three. The continental coasts of the Gulf of Mexico were included in the maps and discussion. The Fleming-Elliott system has been modified and extended in some of its aspects for use in the present study as the geo-oceanographic classification system. Changes in their mapping of the Gulf coasts include the introduction here of young orogenic sectors and the relegation of biogenous coasts to a secondary condition imposed on a framework of regional geologic and geomorphic types. In the latter instance, the suggestion made by Shepard (1948, pp. 78–79) is followed that a regional classification could be made by using large subdivisions such as coasts with young mountains, old mountain ranges, broad coastal plains, glaciated coasts, and such specific but less common items as volcanic coasts and tableland coasts.

Space does not permit including here an elaboration of the detailed genetic-geomorphic classification systems. As detailed knowledge of many coasts accumulates, including coastal plains such as those of the Gulf, the list of the distinctive small-unit features becomes encylopedic and the classification headings numerous, beyond the simplicity desired (Lucke 1938) for text-book and lecture purposes.

Definitions.—The shoreline is the line where land and water meet. It moves back and forth over the shore or shore zone. The shore on a beach has been defined (Beach Erosion Board, Corps of Engineers, U. S. Army) as the zone between mean low tide (or lower low tide) and the inner edge of the wave-transported sand. The lagoonal shore is that of the tidal bays and lagoons. Estuaries are tidal stream courses. Their shores are not studied here except where they are embayed. On some coasts there are extensive, muddy shore-flats. Tidal flats are properly those within the range of normal gravitational tides. In some places winds blow the water across broad, gently sloping wind-tide flats[5] that extend inland from the true shore, hence, beyond the high tide limits for gravitational tides, and have been floored by deposits left by the water.

The coast is a zone of indefinite width back of the shoreline that is affected by or closely affects offshore or shoreline processes and forms. The waters lying near the coast where the effect of a shallow bottom is felt may be called coastal waters. The continental shelf (fig. 13) is a submerged, gently sloping plain that extends the continent oceanward to varying depths ranging, generally, between 40 and 100 fathoms. The shelf is terminated seaward by the steeper shelf slope that descends, in places precipitously, to the depths. Additional definitions will be given in later paragraphs when the barrier island, the shelf and its equilibrium profile, and the mangrove coastal ridge are discussed.

New and undescribed types.—New types recognized on the shorelines of the Gulf of Mexico which will be readily understood from previous geomorphological knowledge are (1) the drowned karst (sub-aerial limestone solution topography) of parts

[4] Shallow water or nearshore zone. Some writers use "inshore" for lagoonal and estuarine environments.

[5] New term.

of Florida and the Yucatán Peninsula (fig. 12; fig. 14, sector 2.1); two minor forms: (2) sand dunes briefly drowned by exceptionally high tides; and (3) wind-tide flats, previously described. Other new types that form striking features on the coast of southern Florida and the Yucatán peninsula, are (1) the great mangrove barrier ridge (fig. 12; fig. 14, Sector 4.1); (2) the irregular mangrove coastal lagoon between the mainland and the ridge, (3) the drowned lacustrine plain of the Bay of Florida (fig. 14, Sector 4.1 north of Florida Keys and east of Cape Sable; fig. 15) as interpreted by the writer, with former lakes of marsh or swamp now invaded and enlarged by salt water, and (4) what the writer believes is the same type of coast slightly elevated (elevated lacustrine plain) to form the pocket harbors (Hayes, Vaughan, and Spencer, 1901) of northwestern Cuba (fig. 12; fig. 14, sector 3.1). The present paper does not offer an opportunity for full critical discussion of these new types.

Besides the distinctly new types of shoreline and coast, noted here, a number of fairly well known geomorphic forms were found which have not previously been included in shoreline classification lists. Prominent examples for the northwestern Gulf coast are the broadly to roundly embayed drowned-stream valley with shallow, pan-shaped depositional bottom previously described and investigated by the writer (Price 1947) and the drowned deltaic topography (fig. 12, between Birdfoot delta of Mississippi and Lake Pontchartrain) described by Russell (1936, figs. 6, 7; 1940).

SOURCES OF INFORMATION

Published articles include (1) the numerous detailed geological reports and maps on coastal land areas in the United States[6] with a few generalized and regional reports on those of Mexico and Cuba, (2) shoreline and coastal studies of the United States Army Engineers, (3) a few ecological studies of coastal areas chiefly in Florida and Louisiana, (4) progress reports of the oceanographic survey of the Gulf of Mexico being conducted by the Department of Oceanography of the Agricultural and Mechanical College of Texas (Leipper, p. 125) and progress reports on investigations of sedimentation and other shallow water conditions of the northwestern Gulf of Mexico by the American Petroleum Institute and similar commercial projects. Among scattered reports on previous oceanographic cruises yielding shoreline or shallow water data (5) is a study of foraminifera in bottom sediments by Phleger and Parker (1951). Much geographic and some geomorphic information is found in Tamayo's (1949) extensive text and atlas of the general geography of Mexico.

Important raw data, some of which are listed in the following paragraph, include (7) topographic maps and air photographs of the land, (8) original Federal hydrographic surveys, including some old surveys of the British Admiralty, (9) navigation and (10) aeronautical charts made from these sources, with (11) the coast pilot and sailing directions handbooks of these organizations, and (12) bottom-sediment charts of the shelf of the northern Gulf. Topographic data are scarce outside the United States and of unequal detail and coverage for the different States. For Mexico, air photography made by the United States and Mexican governments is available under restrictions. The Cuban hydrographic organization has issued a coast pilot (Derrotero) containing new coast charts.

Charts and other aids in study of coasts.—For any detailed study of these shorelines it is necessary to have first, a set of nautical charts. Figure 12, a finding map for this study, is drawn on the base of the general chart for the Gulf. The less accurate and detailed these aids are for any coastal sector, the more they need to be supplemented by air photography, topographic maps and geologic reports. The following charts are recommended.

U. S. Coast and Geodetic Survey Nautical Charts (U. S. Shores).—General Charts, 1002, 1007, 1290: Sectional Charts 1113–1117; Coast Charts 1249–1280. For special details, some of the large-scale charts of islands, harbors and canals, and Chart A634. See catalog: Serial No. 665.

Hydrographic Office, U. S. Navy, Nautical Charts (Mexico and Cuba).—General (coastal) Charts 1125BS, 1126, 1126BS, 2145, 2056, 0966, 5487. See catalog: Pub. I–N.

Marina de Guerra, Departmento de Inspeccion, Officina Hidrografica, Republica de Cuba.—Derrotero de la Isla de Cuba (sailing directions). Parte Segunda, 1951, 173 pp. 21 figs. has coast

[6] Most complete for Florida and Louisiana.

charts from recent surveys done on thin paper, bound in the book. Soundings and underwater contours are given to depths of from 30 to 60 brazos de agua (Cuban fathoms).

World Aeronautical Charts, U. S. Air Force (Mexico and Cuba).—Charts 522, 586–589, and 643–645. See: Aeronautical Chart Catalog, Coast and Geodetic Survey.

Topographic Maps, Air Photographs and Geological Reports.—The U. S. Geological Survey publishes a series of key maps for the United States, Alaska, and Insular possessions showing the status of topographic mapping and air (aerial) photography, including mosaic sheets and with some geologic mapping. State maps showing the areas covered by all published geological reports and articles are available for some States from this agency. The State geological surveys and bureaus also furnish lists of their publications. The Geologic Map of North America, Geological Society of America, 1946, and the American Geographical Society's Map of North America are useful regional aids, besides State geologic and topographic maps.

Areal summaries of oceanographic data.—Since Vaughan's (1937) survey of information available in this field no general key maps have been published. Articles on geological oceanography of coastal areas are now listed in geological bibliographies.

ACKNOWLEDGMENTS

The writer is indebted to a large number of persons and organizations too numerous to list here. Valuable aid was received from the State geological surveys of Florida and Louisiana, and some former members of the latter; several members of the United States Geological Survey; officials of the Coast and Geodetic Survey, Hydrographic Office, photographic branches of the Army, Navy, and Department of Agriculture, and the corps of Engineers; geologists of the Mexican federal geological survey and petroleum development agency, as well as numerous individual geologists, biologists, ecologists, and other persons familiar with remote and little-known parts of the shorelines of Mexico, Florida, and Louisiana. To his colleagues in the Department of Oceanography of the Agricultural and Mechanical College of Texas, the writer is deeply indebted for orientation and guidance in oceanography during the years of 1950–53, as well as for specific information and aid. The development of the research on which this condensed paper is based was followed closely by Warren C. Thompson and Charles C. Bates, while doing research in the Department, with whom many helpful discussions have been held. The impetus in the development of the geo-oceanographic classification here used, as has been said, came from the manuscript by R. H. Fleming and F. E. Elliott.

STRUCTURAL AND REGIONAL GEO-OCEANOGRAPHIC APPROACH TO SHORELINE DESCRIPTION AND CLASSIFICATION FOR GULF OF MEXICO

COASTS AND HINTERLAND

The Gulf provides a good example of the well-recognized relation (Weaver 1950) of the topography of the hinterland to the width of coastal plains and continental shelves (fig. 13).[7] The geologic structure of any hinterland largely controls its topography and has a direct or indirect effect (Suess 1888) on the character and positions of shorelines. These factors are dominant in determining the drainage and hence, the transport of sediment from the land to coastal areas.

[7] Taken from Price (1951 b).

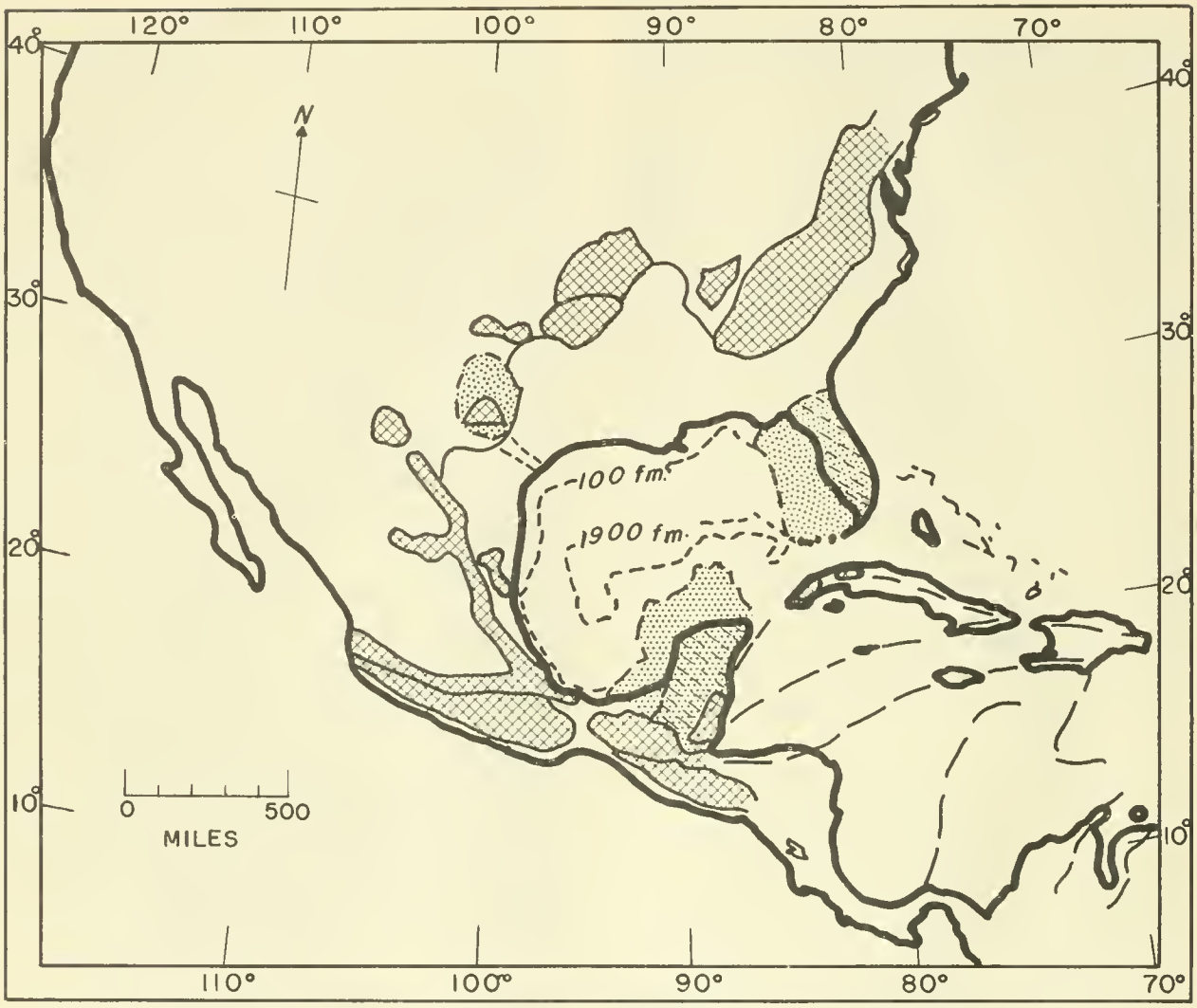

FIGURE 13.—Major geologic structures exposing uplifted rock masses surrounding Gulf of Mexico. Cross-hatched, folded sedimentaries, granitic areas, volcanic belts. Stippled, uplifted arches or horsts. Stipple and dash, emerged parts of arches form limestone plateaus at south and east. Under-water contours, 100 and 1,900 fathoms, the former out-lining the continental shelf, the latter, the Mexican Basin (Sigsbee Deep). Long broken lines, axes of arcuate Caribbean folding (axis of Gulf coast geosyncline, supposedly along northwest shore, not yet located. Scale: Hundreds of miles.

REGIONAL COASTAL TYPES

YOUNG OROGENIC COAST

Where geologically young mountains (Tertiary to Quarternary) closely border the coast (Umbgrove 1947, pl. 5), as in Cuba and the southwestern Gulf coast in Mexico (figs. 12, 13; fig. 14, Sector 3), coastal plains and the continental shelf are absent, narrow or of irregular width, and the shelf tends to be rocky with shoals and irregular elevations (Fleming and Elliott 1950) as well as somewhat steep (slope greater than about 5 feet per statute mile). Sand and mud[8] occur on the shelf and mud along the outer margin and in shelf deeps. The coast may have alternating narrower erosional and wider depositional sectors, the latter with smooth shorelines and bottoms, the former with uneven surfaces. These coasts and shelves are unstable and subject at any time to earthquakes, fracturing and warping of the crust.

[8] Sediment terminology used is that of the coast charts. "Mud" is a field term implying no accurate knowledge of the clay fraction.

Young orogenic coasts have their shorelines dominantly parallel (concordant, Suess 1888) with the structural trends (folds and faults) of the mountains. The Gulf provides no examples of coasts where the shoreline is more than very locally discordant with the structural trends on land.[9] This accounts to a large extent for the almost complete lack of islands in the Gulf other than sandy barriers close to shore, karst islets of Florida, some lava-rock islets in Sector 3 in Mexico, and coral and detrital reefs on shoals. From the meager data of the charts we conclude that, because the Mexican mountains are mostly not younger than Miocene, coastal sediments have built out around or otherwise protected most of their outpost hard rock folds from the Gulf. However, a large mountain range projects eastward under water some 50 miles off Tampico and two parallel mountain ridges trend northwestwardly from the edge of the continental shelf off the Rio Grande delta.

The Tertiary mountains of Cuba (Palmer 1945) rise from a short distance back of the coast. The folded rocks come down to the coast or are overlain there by a thin cover of younger deposits. The island may be divided into several areas of different tectonic structure, but overthrust folds rising up to the south dominate some sectors, as in the extreme west. The Gulf bottom off the north coast descends at angles of 4° to 6° or more, a slope which conforms fairly well to some of the folds. A narrow shelf occurs only where fringing reefs have grown up with a rising sea level to form barrier reefs, so that the lagoon has been filled to a shallow depth with sediment and organic growths (3.2 Sectors, fig. 14).

The drainage of northwestern Cuba is largely southward, so that only small streams enter the Gulf and the coralline lagoons. The sedimentation along the northwest shore has, therefore, been negligible except where coral reefs and mangrove growth have trapped marine and land-derived materials. An erosional sector occurs between the barrier reefs east and west of Havana.

The Sierra Madre Oriental, the eastern cordillera of Mexico, slants southeastward toward the coast, one of the outpost folds in limestone rock making a minor protuberance at Punta Jerez (fig 13).[10] The coastal plain becomes gradually narrower southward from the delta of Rio Grande. It is, however, as much as 60 or more miles wide in places.

The Southern Volcanic Range of Mexico (Sierra Neo-Volcanica, Tamayo 1949), a zone of Tertiary-to-Recent volcanic peaks, runs from the Pacific coast due east through Mexico City to form the broadly protuberant Jalapa Salient north of Veracruz at 20° N. Lat. A similar salient south of the city, that of San Martin Tuxtla, separated from the range, may be geologically associated with it. The range includes some of the greatest peaks of Mexico, including at the east, in sight of the Gulf, Orizaba and Cofre de Perote, reaching elevations of 18,696 and 14,048 feet, respectively, above sea. Between and on each side of these salients are sedimentary embayments (fig. 14, 3.2) with fairly broad coastal plains. Only a narrow belt of low shoreline deposits seems to be present along the fronts of the volcanic salients. These salients are composed of confluent and overlapping flows of volcanic rocks, some of which make small jutting points at the shoreline. Of these, Roca Partida and Punta Delgada have cliffed faces reported to be 1,000 feet high, with islets of lava rock.

There are several volcanic peaks in the San Martin salient, including San Martin Tuxtla, which has been active in historic time. On air photographs of this sector, the writer counted some 20 small cinder cones aligned in a zone about 10 miles wide and 40 miles long parallel with the coast. One of the cones stands in the intermountain Lake Catemaco with its crater invaded by the water.

The continental shelf off the orogenic coast of Mexico is poorly mapped. It is narrow and, where mapped, the gradient is convex, becoming steep, like that near the outer edge of the shelf of Texas and Louisiana. The grain sizes of the sediments, so far as is revealed by the data on the charts, decrease more regularly outward than on some better-known orogenic coasts, as that of California where there are separate offshore sedimentary basins both on and off the shelf, each with its own sedimentary distributional pattern. The small size of the sub-aerial drainage basins where mountains stand near the coast has

[9] Discordant coasts are found today chiefly where old mountain areas, as from New England to Newfoundland, have been drowned by sinking of coasts under load of Pleistocene ice sheets.

[10] The convexity here is exaggerated on H. O. Chart 2056 as compared with the later W. A. C. 589, made from a photographic base.

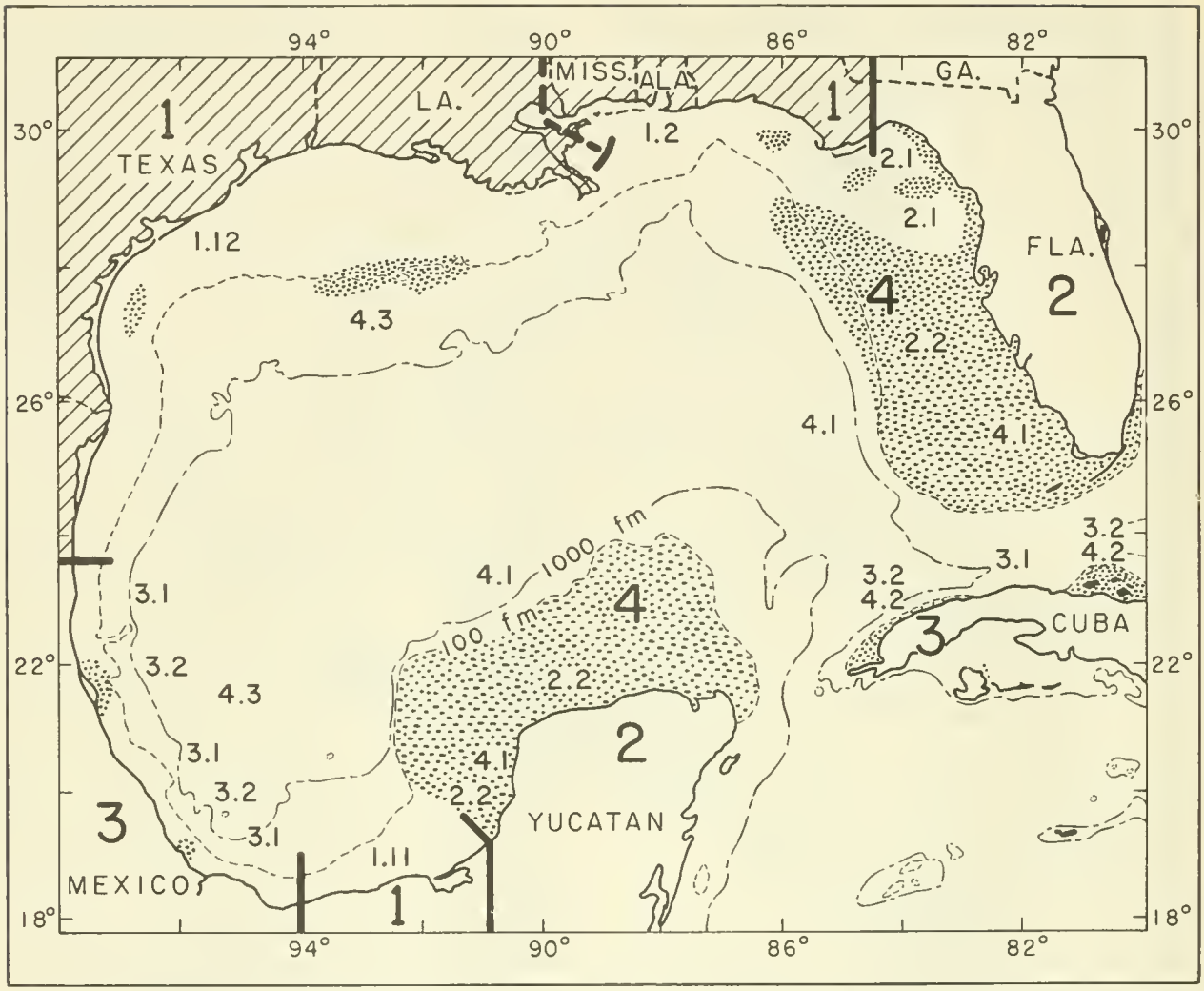

FIGURE 14.—Regional geo-oceanographic classification, shorelines and coasts, Gulf of Mexico: 1, alluvial coasts; 2, drowned limestone plateaus; 3, young orogenic coasts; 4, biogenous (organic) development on various coasts. Sub-sectors: 1.1, deltaic coasts, with 1.11, unentrenched simple deltaic plain, and 1.12, entrenched and embayed compound deltaic plain. 1.2, terraced deltaic coastal plain; 2.1, unsimplified to little simplified drowned karst; 2.2, limestone karst with beaches; 3.1, erosional, and 3.2, depositional, orogenic coasts; 4.1, broad shelf; 4.2 shelf absent to narrow; 4.3 lesser biogenous development (more extensive than shown). The two southerly Mexican 3.1 Sectors are volcanic salients.

been shown to restrict coastal sedimentation. This is true here, in that the shelf is wide off the several sedimentary salients, but narrow in front of the coastal mountain salients.

ALLUVIAL COASTS

Where the closest mountains, usually old mountains, are located far or moderately far inland (Umbgrove 1947, pl. 5), the runoff and sediment load from the lands has been large and long continued, interior plains are succeeded by broad coastal plains and continental shelves, and the coast is of the deltaic (Fleming and Elliott 1950) or alluvial coastal plain type. On such a coast, after sufficiently long stillstand, shelf bottoms are smooth except toward their outer margins, organic reefs are inconspicuous, few or absent, and shorelines are smooth or irregularly deltaic (fig. 13, and No. 1 Sectors, fig. 14). Sediments here are generally of even distribution to somewhat spotty (Lynch, fig. 16). Sands extend from shore out to about 5 or 10 fathoms, followed by silt or sand and mud (charts), with mud further out to the edge of the continental shelf. Mud or silt

may come in very close to the mouth of a deltaic river that drains a large basin. The chief exceptions to the outward banding of sediments (Emery 1952) are any coarse sediments of local organic or chemical origin, or, along the northwestern shelf of the Gulf, sediments on mounds believed to lie above buried intrusive salt domes (Shepard 1937 b).

The alluvial sectors of the Gulf of Mexico (Sectors Nos. 1.11, 1.12, and 1.2, fig. 14) have smooth shorelines with sandy beaches on the mainland, or on barrier islands (Price 1951 a). The beaches may be more or less interrupted by deltas of varying degrees of protuberance and shoreline irregularity (Russell 1940; Bates 1953). Offshore, the alluvial sectors have broad, smooth continental shelves, 130 miles wide at the maximum, with relatively steep inshore shelf-bottom profiles (fig. 15, Sector VII) and a rather uniform gradation of sediment from sand (generally inside the 5- or 10-fathom depth contour) to sand-and-mud, with mud at the outer margins. The elevated mounds on some outer parts of the northwestern shelf have nodular algal limestone on their tops and possibly some coral.

Subsectors, alluvial coast: terraced deltaic plain.—Sector 1.2, Alabama, Mississippi, and western Florida (fig. 14), has a fairly steep coastal plain,[11] with two Pleistocene-and-Recent deltas (Apalachicola, Pascagoula, and Pearl), a minor amount of embayment of drowned stream valleys and a reported series of low, parallel elevated shoreline scarps (Carlston 1950). In places, the younger two of these have roughly parallel Pleistocene barrier islands and coastal lagoons (MacNeil 1950) in part entrenched by drainage and embayed. This coast is like that of the southern Atlantic coastal plain of the United States, with which it has a common geologic history. These similarities exist because of the position of the old (Paleozic), almost entirely quiescent Appalachian mountains fairly close (90 to 150 miles) to the coast but not in a bordering position. Drainage basins extending from the mountain front across the coastal plain are small in relation to those of the deltaic 1.12 alluvial coast. The large cuspate Pleistocene-Recent Apalachicola delta and the long, broad, and shallow Mobile Bay are striking features of this coast

[11] Eight feet per mile near the coast in some places.

Broadly embayed deltaic coastal plain.—Sector 1.12 (fig. 14), the coast of Louisiana, Texas, and part of Tamaulipas, receives the drainage of some ten major rivers. Three major Recent deltas now reach the Gulf; the Mississippi-Red, Brazos-Colorado, and Rio Grande deltas. A very broad, gently sloping deltaic coastal plain (Barton 1930) has been built, forming a fully concordant coast (Suess 1888). Coastal plain deposits form a new structural (monoclinal) trend in front of the abrupt southwestern ends of Appalachian folds once projected into the broad Mississippi embayment.

Sector 1.12 (fig. 14) is deltaic except between arcuate delta fronts where the active barrier and the Pleistocene Ingleside barrier island (Price 1933) with their parallel, active and entrenched coastal lagoons form a diversified inner coast transected by many broadly drowned and embayed stream valleys (Price 1947). There are, thus, intermittent terraced riverine plains between adjacent protuberant Recent deltas. Behind the terraced belt are continuously overlapping and coalescing Pleistocene deltas with their surfaces slightly up-warped inland. The great protuberant Mississippi-Red delta (Russell 1936; 1940; Bates 1953) dominates the eastern part of this sector both at the shoreline and on the shelf where large shoals seem to indicate submerged deltas. A minor feature of the deltaic coast is the saline marsh (paralic) environment described on a later page with the biogenous environments.

Saline plain of Rio Grande delta.—A broad, treeless, saline plain, the Jackass Prairie of Cameron County, dominated in the native state by coarse, bunchy *Spartina* salt grass (sacahuista), stretches inland across the Recent delta north of the natural levees of the present Rio Grande course for a maximum distance of 10 miles. The Gulfward edge of the plain is honeycombed by saline lagoons lined on their lee (N., NW., W., and SW.) sides by clay dunes (Coffey 1909, Price 1933, Huffman and Price 1949). The soil of the low deltaic plain is made heavily saline by wind-blown (cyclic) salt contained in clay pellets and dust blown from the saline tidal flats of the lagoons. These flats undergo strong deflation during the warm months. Sand-sized pellets of flocculated saline clay accumulate on lee shores to build the dunes, while saline dust passes over the 30-foot-high dunes under the strong steady hot winds of the warm months.

From detailed topographic data it is estimated that about one-fifth of the wind-blown clay excavated from playa lake basins is caught on the dunes as sand-sized pellets and the remainder passes inland as dust. The saline plain is narrower in Willacy County to the north where the Recent delta and the zone of playas and dunes is narrower than to the south near the Rio Grande.

Unentrenched deltaic sector.—Sector 1.11, the coast of Tabasco and parts of Veracruz and Campeche, Mexico (figs. 12, 14), is a simple deltaic coast with a tropical rain-forest and fairly wide tidal streams that are not embayed. The large Laguna de Terminos is a delta-margin depression, a feature which Bates (1953) thinks is normally a nondepositional basin. Sinking by compaction, former entrenchment and enlargement by wave and current scour are factors that aid in shaping some of the delta-margin basins. This sector has a broad, gentle deltaic plain, abundantly crossed by innumerable courses of the Tonala, Seco, Grijalva, Teapao, Usumacinta, San Pedro Y San Pablo, and Palizada Rivers. These courses are grouped into two main deltas; the Seco-Grijalva delta at the west, with a broadly and symmetrically bowed shoreline, and the asymmetrically bowed Grijalva-San Pedro Y San Pablo delta at the east. The latter has a small cuspate mouth.

DROWNED LIMESTONE-PLATEAU COASTAL PLAINS

Continental or insular shelves may exist off the above-water parts of oceanic shoals appearing as island groups or as peninsulas attached to continents. Very broad shelves, upwards of 100 miles wide, border the peninsulas of Florida and Yucatán in the Gulf (fig. 13 and No. 2 Sectors, fig. 14). These low peninsulas are great uplifted limestone shoals, now partly drowned limestone plateaus. Their origins have been discussed elsewhere (Price 1951b). The surfaces of these plateaus, both above and below water, show a young rolling karst topography of limestone solution with solution-basins and sinkholes. Surface drainage is locally absent and is supplemented by underground water circulation moving through solution channels. The Florida limestone is abundantly fissured, at least at the northwest (Vernon 1951).

The plateau peninsulas are terraced limestone coastal plains. They have delivered a minimum of land-derived detrital sediment to the shelves, so that, under tropical climates, these shelves in places abound and probably have long so abounded in great coral reefs (F. G. W. Smith, p. 291) and some reef-like bars and sand keys of shell detritus.

The sinkhole topography of the limestone plateaus is of subaerial origin, now modified in a broad belt near the shoreline, both above and below water, by coastal deposits (Vernon 1951)[12] and an undetermined amount of solutional activity (Fairbridge 1948). There are a few relatively narrow, submerged stream valleys. Submerged subaerial karst basins are, so far as known, only shallowly filled with a foot or two of sediment, yielding poor anchorage for ships. Offshore bottom slopes of the inner half or more of the continental shelf are very gentle (fig. 15, curve 6) to moderately gentle (fig. 15, curve 4), ranging from about 1.5 to 2.5 feet per statute mile. For a few miles offshore, there are many, irregular, shifting bars of shelly sand.

The limestone-plateau coasts have three types of subsectors: slightly elevated drowned karst salients of a low marshy coast (2.1), beach-bordered (2.2), and mangrove-ridge (4.1) shorelines. These show shoreline modification and smoothing ranging from a virtual zero modification through incipient planation to nearly completely smooth beach-bordered coasts. Coastal marsh and swamp of the limestone plateaus are abundantly channeled perpendicular to the shoreline by tidal scour. The tides are higher on the peninsula coast of Florida (range 2 to 4.5 feet) than on any other part of the Gulf shoreline. Inshore on the drowned karst coast, and offshore on it and on the other subsectors of the limestone plateaus, we have the so-called carbonate environment of the continental shelf (Trask 1937).

DROWNED KARST SHORELINE SUBSECTOR

Subsector 2.1 (fig. 14), along the northern coast of peninsular Florida north of Anclote Keys, near Tampa, has a new type, the drowned karst shoreline. Short convex areas have an intricate, crenulate shoreline with many small shoreline basins and archipelagoes of stony islets. Much of this karst shows, on the scale of the navigation charts, no modification by marine agencies. This entire subsector lacks embayed drowned stream valleys

[12] Zones of submerged bars and their uplifted counterparts on elevated terraces.

and sandy beaches (Martens 1931) except short, elevated stormbeach ridges and sandy beaches on some of the Cedar Keys archipelago at 29°10′ N. Lat. These latter beaches (Martens 1931) are somewhat muddy and unlike those of glaringly white sand on the front of the Apalachicola delta, Sector 1.2, and westward from it in Florida.

With this drowned karst coast of Sector 2.1, there are areas of transversely channeled marsh 2 to 3 miles wide occupied by grassy vegetation and forested swamp. This swamp is probably mostly saline. Patches of mangrove swamp occur in the southern part of this Sector.

The scattered mangrove swamps with offshore oyster reefs to be described mark a minor extension of the biogenous environment (Sector 4, fig. 14).

The drowned karst coast is conspicuous for its many and unique marine oyster reefs, located along a shallow-water zone extending outward to a distance of a mile or two from shore. *Crassostrea virginica*, the North American oyster of commerce, is notably lagoonal and estuarine, commonly being confined to brackish water environments by its marine-water foes. Only along parts of the Gulf coast are living reefs of this species known in oceanic waters in North America. On Sector 2.1, the highly fractured and channeled limestones of Florida are filled inland with fresh water to a considerable height above sea level. The slope of the groundwater surface (piezometric) toward the coast indicates a movement of underground water in that direction. Also, along much of the coast of Sector 2.1 there is an artesian groundwater head of about 10 feet near and at the shoreline (Cooper and Stringfield 1950, fig. 14). This pressure-head forms springs in the stream mouths and stream beds, as well as offshore.[13] The absence of land-derived sediment in these streams during most of the year and the protected nature of the shelf waters leave the water of the Gulf brackish here. Off the mouth of Atchafalaya Bay, Louisiana, oyster reefs also grow in the Gulf out to a distance of 3 to 5 miles, with the fresh water of the river mixing with Gulf water to produce a brackish environment.

Beach-bordered karst subsector.—Sector 2.2 (fig. 14) is represented both on the central coast of peninsular Florida and on the coast of the Yucatán Peninsula. On Florida, the sector has fairly continuous sandy barrier islands and barrier spits with some mainland beaches. This sector extends from Anclote Keys near Tampa at the north to Cape Romano at the south. The drowned karst lies behind the beaches and the coastal lagoons of the sandy barriers. The lagoons are bordered by mangrove swamp and with the karst depressions more or less filled with sediment and marshy growths.

The beaches of this sector (Martens 1931) have much shell material but also quartz sand. The quartz is derived from elevated sandy Pleistocene beach deposits of the elongated dome-shaped summit (300 feet or more) of the peninsula, which lies immediately inland, and from a sandy limestone formation that has been almost removed by embayment of several streams to form the broadly embayed harbors of Tampa Bay and Charlotte Harbor. These harbors are the only embayed, drowned, stream valleys of the Gulf coast of the peninsula, except the moderately widened tidal portion of Caloosahatchee River, nearby. The shelf-bottom slopes more steeply off this sector (2.2 feet per mile, fig. 15, curve 4) than it does farther north on Sector 2.1.

Cape Sable (fig. 12) protrudes into the Gulf where Florida Bay extends eastward at the end of the mainland of the peninsula. This major shoreline bend produces a convergence zone for waves, swell and currents with the local wave attack necessary to develop a beach, keeping the shore free of mangroves. The beach plain has cuspate points and encloses narrow lagoons behind it. The beach sand is presumably mainly shelly.

The oval area of plain behind the sandy beaches and the lagoons of the Cape is somewhat marshy. The origin of the broad, irregular lagoon known as Whitewater Bay, lying several miles inland from the beach is linked with the delivery of a concentration of drainage to a marsh. The bay is heavily fringed with mangrove swamp.

The beach-bordered subsectors (2.2) on the Yucatán Peninsula include the northern coast and the short Campeche–Champoton sector at the west. The northern coast has barrier islands and a number of slightly disconnected barrier spits which extend westward from moderate projections of the shoreline. Pinnacles of limestone

[13] Data on charts and reports of aviators via V. T. Stringfield, letter of 1952.

several feet high protrude through the beach in places (Sapper 1937). Marshy, swampy, and partly mud-filled coastal lagoons lie behind the barriers. They are extensively occupied by mangrove swamp forest. These lagoons are called "rivers" on some maps. They were formerly thought to form a continuous inner waterway across the north end of the Peninsula.

The short beach-bearing sector in the Campeche coast between the towns of Campeche and Champton (fig. 12), seems from air photographs and ground-elevation figures (20 feet to the north against 400 to 500 feet in the block) to be an uplifted fault block of limestone with entrenched stream valleys floored by narrow alluvial plains. The Gulf ends of these alluvial deposits have sandy-to-cobbly pocket beaches. Observers report seeing large blocks of limestone on some of them. One report, probably, erroneous, calls some of these blocks and a nearby outcrop "igneous" rock.

BIOGENOUS ENVIRONMENT

Where, on the coasts of the Gulf, land-derived sediments have been and are now scarce, sediments of organic origin with large marine organic structures become conspicuous. Such a biogenous environment (fig. 14, Sector 4) (Fleming and Elliott 1950) may vary, here and there, from a brackish lagoonal and inshore environment to a marine environment with waters of normal salinity or salinities somewhat above average (Trask 1937). Where the water is now, or has lately been, warm, tropical and of at least normal marine salinity, coral reefs thrive. The physical limitations of this environment have been long and widely discussed.

The biogenous environment is an oceanographic condition existing as an overlay on the basic geological coastal structures. It may occur on any type of shoreline where, and so long as, the requisite sedimentary and oceanographic conditions previously mentioned occur. The biogenous environment includes the carbonate environment, where Mollusca and corals are conspicuous among the sedentary organisms, and the paralic or marine swamp and marsh environments, such as those of the mangrove and saltwater grasses and reeds.

It may be that, with further analysis, a fundamental geological coastal type of biogenous nature may be recognized. Thus, the limestone peninsulas of Florida and Yucatán may, from the historical point of view, be considered geologically biogenous, since the limestones have been built up for millions of years under dominantly calcareous biogenous conditions. The Cuban coast, and the Gulf coast of Mexico west of the Yucatán Peninsula, are today only superficially biogenous, as the organic growths and sediments form a mere patchwork skin on the rock folds. Limestone series several thousands of feet thick among the folded and faulted rocks of Cuba, however, show that the site of the island was biogenous for millions of years. Deposits of argillaceous (clayey) shales and the great earth-deforming (tectonic) events, were major interruptions in the carbonate type of biogenous environment in Cuba. The structural conditions of Cuba today overshadow, for geologists, the biogenous history.

Carbonate subdivisional environment.—Subsectors of the biogenous coasts (Sectors 4) present a variety of structures and bottom types. Coral reefs and the carbonate environment in general occur on both broad (fig. 14, 4.1) and narrow (4.2) shelves. Large shelf areas have a conspicuous bottom-dwelling population. Among these, sponges are conspicuous. Actively growing coral reefs (Smith, p. 292) include fringing and barrier reefs on Cuba and a barrier reef along the outer side of the Florida Keys. This coral barrier runs along the edge of the shelf facing the Straits of Florida at the far southern end of the peninsula. Fringing reefs are also found here and there on other coastal sectors, as near the mouths of streams on the Mexican coast (Sectors 1.11, 3.1, 3.2) and on 4.1 on the Yucatán Peninsula. The great Colorados Barrier Reef of northwestern Cuba is fringing at its eastern end but encloses a 15-mile-wide lagoon to the west.

Atolls and atoll-like coral reefs of more or less tabular form occur west of the Florida Keys (Dry Tortugas atoll) and others form a great, discontinuous, barrier range along the northern and northwestern margins of the Yucatán shelf, called the Campeche Banks (Smith, fig. 62, p. 292). The best known of these is the large Alacran atoll. The Marquesas detrital atoll off Florida (Vaughan 1914; Cooke 1939, fig. 31) is not known to have coralline growth, the reef being a group of sand keys of shell detritus formed on the shelf by the strong westward currents and winds. The Mar-

quesas is a great lunate key partly closed at the southwest by a series of smaller lunate keys curved oppositely to the major key and built by secondary currents from the west-southwest. The living barrier reef of southern Florida in front of the main Florida Keys stands in about 5 to 7 fathoms of water. The Colorados Barrier Reef of western Cuba stands in about 5 to 6 fathoms. The barrier range off northern Yucatán, however, stands in 20 to 30 fathoms, nearer to the edge of the shelf than to the mainland.

The Florida Keys are partly coralline, partly of other origin (Cooke 1945, pl. 1, and 1939, pp. 68–72). The main eastern Key range is considered to be a former barrier coral reef of the elevated Pleistocene Pamlico (25-foot) shoreline, now emerged and dead. Its highest present natural ground elevations are said to be about 18 feet above present mean sea level. This Key range ends to the southwest in the Boot, Marathon, and Vaca group of Keys. Westward along the line of the Keys, there is a large emergence of the Miami oolite limestone stratum to the present intertidal zone, somewhat built up, in places, by mangrove peat and marl. Marine carbonate and paralic deposits combine to form the Pine Island group of Keys. This low island mass has been broadly and abundantly channeled in a northwest-southeast direction by the strong tidal currents produced by the regularly recurring tidal difference of 2 to 3 feet between the Gulf and Florida Straits. Key West is the western terminus of this group of channeled-shoal Keys.

West of Key West and the Pine Islands lie the small Sand Keys (Davis 1942) where the main Miami oolite shoal lies below or mainly below low tide. These Sand Keys only sparingly fill the gap between the Pine Island Keys and the large Marquesas atoll.

Scattered coral patches.—The scattered patches of coral growth mapped by various agencies and persons along the northern coast of the Gulf (fig. 14, Sector 4.3), far out on the shelf are not well known. These notations may refer to growths on the tops of small salt-dome-like seamounts found along the edge of the shelf here. Studies by H. C. Stetson show that nodular algal limestone balls are common on the tops of some of these small seamounts. Specimens of solitary corals, possibly from the sea areas, are found sparingly upon the beaches. Coral patches occur widely as bottom growths off the central peninsula coast of Florida.

Paralic, or marine marsh and swamp subdivisional environment.—In the biogenous environment, as here defined, grassy to reedy marsh is dominant between the convex areas of drowned karst shoreline (fig. 14, Sector 2.1). It is also scattered among the mangrove swamps. The mangrove swamp forests (Davis 1940, 1942) form a conspicuous marginal coastal belt on the inshore sectors noted (4.1, fig. 14), and occur prominently in the lagoonal habitat on 4.1 and 4.2 Sectors.

Fresh-water marsh (paludal environment) has some of its most extensive known developments on the broad, very gently sloping coastal plain of southern Florida inland from the marine mangrove shoreline. The paludal areas include the famous Everglades and the almost as well known Big Cypress Swamp.

Marine marshes (paralic) are conspicuous in places in a relatively narrow zone along the coast of Louisiana in the deltaic alluvial environment. Here salt grasses (*Spartina*) and reeds have pioneered on deltaic and other shoals. Garden Island Bay, between two mouths of the Mississippi's active bird-foot delta, is reported (Russell 1936) to have extended its shoreline materially by the aid of paralic vegetation. Here, again, extensive fresh-water marshes lie inland in a very gently sloping coast from the more notable saline marshes. On the steeper deltaic coast of the western Gulf, shore and coastal marsh are narrow and relatively inconspicuous.

Mangrove swamp growth.—Charts of the near-tropical coast of Florida (4.1, fig. 14) south of Cape Romano (1113, 1253, 1254) and north of the Bay of Florida, and air photographs of a part of the west coast of the Yucatán Peninsula (4.1), show a broad, belted disposition of saline mangrove swamp forest with an irregular brackish lagoon or line of lagoons landward from it. This arrangement seems to be unique for North America and for those parts of the Antilles which have been studied by the writer. It depends upon the presence of a broad, shoal continental shelf in a tropical or near-tropical sea. Lesser mangrove growths on lagoonal shores seem to be incomplete approaches to this disposition of the swamp.

Mangrove swamp forests extend along the coasts of the biogenous sectors (4, fig. 14) with an extension on the drowned karst (2.1), and on the

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southwestern Gulf coast (1.11 and 3). The swamps occur either in lagoons or on outer coasts that lack beaches or cliffs. It is along the beachless and cliffless coasts, in quiet shallow waters, that the unique mangrove ridge and lagoon are found. Davis (1940) reports the growth on Florida as one of the greatest known. The tropical and near-tropical mangrove forests of the main biogenous environment are dominated by the red mangrove (*Rhizophora mangle*) and the white buttonwood or white mangrove (*Laguncularia racemosa*). Inland from the widely flooded zone, the black or honey mangrove (*Avicennia nitida*) grows. The latter outruns the other mangroves into the marginal tropical regions north of the main biogenous environment. The black mangrove grows as far northwest as the Chandeleur Islands of Louisiana off the eastern part of Mississippi delta and in spots in the Laguna Madre near the mouth of Rio Grande. In the mangrove forests of southern Florida numerous other trees and plants grow with the mangroves (Davis 1940).

The fact that red mangroves build out the shores on which they grow has long been known to geologists (Vaughan 1909). The abundant roots and the manner of seeding on shoals by the floating of well-sheathed seedlings aids these trees in occupying marginal marine and lagoonal areas in protected waters (Davis 1940). The black mangrove, however, seeds immediately under its branches, and tends to grow toward land from a shoreline fringe, rather than outward.

The mangrove barrier ridge and coastal lagoon.—Chart 1113 shows an extremely irregular outer shoreline beginning at the north with the Ten Thousand Islands archipelago. This belt of islands starts at the northwest in the coastal lagoon behind the Cape Romano barrier spit. It then curves to the southeast to end at Lopez River. From Lopez River southeastward to Cape Sable the mangrove swamp of the outer coast is mapped as being much more compact than in the Ten Thousand Islands, and is smoother, but far from regular. It is broken by transverse marshy channels and has, in the northwestern part, an outer line of islets and small peninsulas. From 3 to 8 miles inland, there is a zone of highly irregular, more or less intercommunicating swampy lagoons and channels running roughly parallel with the outer coast. Between the inner lagoons and the outer coast, there is a broad belt of mangrove swamp which is the ridge. Davis shows that the height of the ridge should be a function of both tidal range and the slope of the bottom and adjacent land surface across which the mangrove belt originally spread.

The entire coast southeast of Cape Romano (4.1) is composed of mangrove swamps and lagoons except for the sandy barrier islands, spits and beaches of the Cape Romano barrier at the northwest and of Cape Sable at the southeast. The delineation of shorelines for the mangrove forest is difficult (McCurdy 1947) because of the indefiniteness of shoreline position for a marine swamp, especially where the tidal range, as here, varies from about 2 to 4 feet. East of Cape Sable, there is a mangrove belt along the north side of Florida Bay.

The mangrove peat rests on limestone rock, marl, or shell beds (Davis 1940). The peat section varies from about 5 to 14 feet. Except where it descends into depressions in the karst, Davis thinks that the general average thickness is about 7.5 feet below mean low water. This would place the base of the peat at an average of 8 feet, or slightly more, below mean sea level. The red mangrove seats itself in as much as 2 feet of water, the roots spreading outward somewhat. The seedlings float and ground in a few inches of water. There was in many cores taken by Davis through the peat, an alternation of peat and marl, with an upper marl bed a foot or two thick present in most of the area. The roots of the present swamp trees penetrate this upper marl but without peaty development in it as yet. Alternations of marl and peat in a core may or may not indicate a vertical oscillation of sea level, as they, certainly in some cases, have been due to compaction or minor horizontal shoreline changes under essential stillstand of the sea.

The history of the formation of the mangrove barrier ridge and lagoon may be somewhat as follows: On a broad, well-protected tropical to subtropical shoal coast, especially, as in Florida, where the wind is dominantly offshore but swell and some on-shore wave movement is present, advance of the mangrove forest is assured. The elongated, winged, pod-shaped seedlings ground and take root at any depth down to 6 to 8 inches of water. Root growth may extend as far offshore as a 2-foot depth at low tide (Davis 1940). The dense growth of roots, trunks, and associated veg-

etation, slowly advances seaward by the consolidation of peaty growth and by trapping fine-grained inorganic sediment (Vaughan 1909). Shells are added by the accumulation of small species of Mollusca on the roots (Davis 1940). It may be assumed that the maximum of accumulation of marl, clay, and silt takes place always somewhat forward, that is, gulfward, in the slowly advancing swamp. Storm waters and tidal oscillations combine to permit the up-building of the accumulating swamp materials by these inorganic sediments which, in turn, may promote, at and above high tide levels, a denser undergrowth of the less aquatic plants.

As the zone of maximum arrest and accumulation of inorganic sediment advances Gulfward, lack of accretion or a decrease in rate of accretion in the zone nearer the original mainland permits normal compaction of peat and marl to show in an invasion of groundwater and brackish marine waters. The swamp is abundantly penetrated all along the western peninsula coast by transverse tidal scour channels, permitting Gulf waters to enter the rear zone.

If the foregoing processes and results depict the true history of the formation of the mangrove barrier ridge and lagoon on the western coast of peninsular Florida during the stillstand for the 3,000 to 5,000 years of Fisk's (1944) determinations, then the considerable width of 5 to 10 nautical miles of the mangrove belt is a product of the extended period of time during which approximate stillstand has persisted. If minor oscillations have occurred during this period, then some of the alternations of peat and of peat marl and in the types of peat reported by Davis may have been related to changes of sea level. An end condition of seaward advance may be found where the bottom slopes too steeply, or the growth has finally reached a zone where the processes outlined no longer produce bottom offshore that is sufficiently shoal to support mangroves. Under this hypothesis, we may understand why the mangrove growth on the southern part of the Gulf shore of Florida is exceptionally wide, as the combination of conditions required for the full formation of a mangrove ridge and lagoon are exceptional. Under this hypothesis the rate of Gulfward advance is the ratio between the width of the ridge, 30,000 to 50,000 feet, and the duration of stillstand, 3,000 to 5,000 years. Using the figure 5,000 from Fisk's estimate, we find that the net outward advance of the mangrove forest has been between 6 and 10 feet per year. This is a measurable quantity.

It has been said that Davis (1940) finds the present swamp forest to be resting on and rooted through a surficial zone of marl a few feet thick without appreciable peat deposition in it. Hence, his interpretation that the accumulation of the average of 7.5 feet of buried peat and marl took place mainly during a rise of sea level seems not to conflict with the present writer's hypothesis for forward growth during stillstand. Accumulating datings by the deterioration of radiocarbon may permit a rate of upward growth, less compaction, to be made, Davis having found no means of doing so.

The mangrove barrier ridge and coastal lagoon are similar, in accomplishing appreciable shoreline prograding, to the other barriers known, the barrier island of sand, the barrier coraline reef and the rare barrier oyster reef, noted in the Gulf of Mexico where a large reef of *Crassostrea virginica* forms a bay barrier 25 miles long across the mouth of Atchafalaya Bay.

EMERGENT AND SUBMERGENT SHORELINES OF THE GULF

USE OF TERMS

Johnson (1919) laid much stress, in his shoreline studies, on the determination of whether the features of a shoreline were dominantly those of the relative submergence of a land surface or the relative emergence of a sea bottom. His interest centered in the immediate history of sea level and its effect on shorelines. Others have found it impracticable to discriminate entirely on many coasts between the exact form of the present shoreline and the topography of the coastal zone which has determined major features of both coast and shoreline (Shepard 1937a, Price 1939). This distinction involves the difficulty in determining for each sector whether the several submergences or emergences of the coasts during the Pleistocene have produced its dominant features.

A major shortcoming of the Johnson classification or the way in which it came to be applied was its use of the common and widely developed barrier island as either a major criterion or a

positive indicator (Price 1939, Johnson 1938) of emergence. Later work, here discussed, seems to invalidate this criterion entirely as an indicator of sea-level movement except where it may be found wholly emerged or submerged.

While not finding the concepts of submergence and emergence as valuable for shoreline classification as some others, we may well inquire what features plainly indicate such items of shoreline history.

SUBMERGENT SHORELINE FEATURES

Pleistocene entrenchment of stream valleys.—It is well established that the accumulation of large amounts of ice in the arctic and circumarctic regions several times during the Pleistocene, or Great Ice Age, caused strong lowerings of sea level. The latest well-established major lowering occurred in the late Wisconsin or Würm glaciation and amounted to about 450 feet in the Gulf of Mexico (Fisk 1944, 1952) and the Gulf of Paria, south of Trinidad, Venezuela.[14] In some regions the figure is set at between 240 and 350 feet (Flint 1947). Fisk (1944, 1948, 1952) has shown by borings cited in various reports of the Corps of Engineers that the northwestern Gulf coast had a large number of entrenched Pleistocene stream valleys that have now been filled with sediments. Configurations of branch estuaries show that entrenchment was general in the Gulf. Only on the hard shelf off peninsular Florida are such valleys found submerged and fairly well outlined by depressions. These valleys are marked by depths of as much as 10 to 15 feet on the coast charts off northern peninsular Florida.

Embayed drowned valleys.—Incompletely filled drowned valleys in the Gulf take at least two forms, those in which the branching, dendritic pattern of drowned tributaries is still prominent (Baffin Bay in Texas) and those in which waves and currents have broadened the valley at shallow depth, producing oval, rounded or other equidimensional shapes. The writer (Price 1947) has shown that on the northwestern Gulf coast elongated drowned valleys tend to become segmented by spits and other obstructions, separately embayed by segments and the bay bottoms made flat under a dynamic equilibrium between erosion and deposition. This equilibrium of basin shape is actually the result of the formation of equilibrium bottom-profiles along most bay radii.

Embayment of drowned streams is most prominent in the Gulf on the compound Pleistocene-to-Recent deltaic coast of Texas and southwestern Louisiana. There, the rivers are large and the gradient of the Beaumont is not steep (1 to 3 feet per mile). On the steeper plain of Sector 1.2 (fig. 14), only one large, transverse valley bay (Mobile Bay) occurs. Where the plain is composed dominantly of active deltas or hard rocks or has only relatively minor streams, Sectors 1.11, 2.0 and 3.0, long broadly embayed stream valleys are absent. The writer has further considered local meteorological influences in the shaping of the bays of the northwestern coast (Price 1952).

The harbor of Matanzas, Cuba, is thought to be a drowned valley cut in a structural depression or in a structurally weak zone.

Submerged base of mangrove peat.—Davis' (1940) conclusion that the mangrove swamps and peat of Florida formed during a gradual, more or less uninterrupted rise of sea level from about −8 feet relative to mean sea level has been mentioned.

Drowned lacustrine plain of Florida Bay.—Anaylsis of this unusual type of marine area needs somewhat extended exposition. The entire water area (Trask 1939, pp. 292, 293) is a honeycomb of shallow, rimmed basins individually upwards of 10 miles wide and 11 feet deep, the bottoms bare with a cover of soft marl or shell sand. The narrow rims are of marl and mangrove peat (Davis 1940). The writer's interpretation is that a rising sea moving up and across a very gently sloping shoal surface carried with it a transgressive shoreline zone of mangrove swamp. This coastal swamp belt, the mangrove ridge, moved slowly north and northeastward and is now present along the north shore. This ridge is of irregular shape and the marsh and swamp back of it to the north are now and were probably at all times honeycombed with lakes. Such lakes tend to become enlarged by wind scour if the banks are not encroached on too strongly by marsh and swamp growth. The result is that some large lakes occur among the innumerable small ones.

It is further postulated that, as the Gulf waters invaded the swamp, more and more deeply, vegetation was slowly killed, and the lakes gradually widened by drowning and wave erosion.

[14] Personal communication, T. H. Van Andel.

The outlines of the lakes and rimmed basins of Florida Bay today show the characteristic coalescing of small basins with each other and with large ones, the intervening rims being removed. The lacustrine plain, the so-called bay, with its network of marl ridges prevents the development of appreciable tidal flow and scour in and between basins except along the border of the bay at the south. Here tidal channels have been scoured through breaks in the line of the Florida Keys, locally deepening the rimmed basins.

Statistical study of the relation between width and depth in the rimmed basins shows a rough approximation to the progressive deepening with increasing size characteristic of the bays of the northwestern Gulf (Price 1947). In the Bay of Florida this relation is modified on the southeast by the limiting depth of the hard Miami oölite and at the extreme west by an excess of sandy or marly deposition in the relatively large basins that there border the Gulf. Some of the western basins are completely filled with sediment.

Partly submerged eolian sand plain of Rio Grande delta region.—Stretching inland across the Pleistocene plains of this delta in Tamaulipas and Texas to their inner erosional scarp is a plain of eolian sand, or erg, with scattered dune fields. All, except small blowout fans of bare sand (about 1 by 3 miles in size) and their fields of bare dunes, is stabilized by grassy vegetation, thorny brush and live oaks. The coastal lagoons now form traps for eolian sand blowing inland from the beaches of the barrier islands. Only in droughts is some of this sand able to cross to the mainland over narrow flats that locally close the coastal lagoon. This immense sand plain must have come on shore before the barrier island was formed. The simplest explanation follows that of Daly (1934, pp. 197–201) that large amounts of sand probably blew on some shores when the sea level was low during one or more of the glacial periods. Other possible explanations are that the sand has come from the reworking of successive barrier island sands and other beach deposits or from sandy sediments in the walls and on the floors of entrenched valleys.

EMERGENT SHORELINE FEATURES

Pocket harbors (emergent rimmed basins) of Northwestern Cuba.—Several writers on Cuba (as Hayes, Vaughan, and Spencer 1901) have referred to the purse-shaped or pocket harbors of Cuba. Those of the sector from Havana to Bahia Honda (fig. 12) on the northwest coast are of an unusual, petal-shaped type. They lie in a plain from 3 to 5 feet above sea being upwards of 6 miles long. A small stream usually enters one or more of the several marginal indentations of the small rounded-to-oval basin, not always in the axial position. Other similar marginal indentations have either no appreciable inflowing drainage or receive very slight drainage. Yet well-formed submerged channels converge from all these indentations toward a central channel of tidal type. This channel may be as deep as 8 fathoms. Such harbors do not seem to the writer to be explicable as normal embayments of drowned stream courses or of stream confluences, as some have suggested.

If the coast of Cuba west of Bahia Honda (3.1, fig. 14) is examined on the navigation charts, basins similar to the pocket harbors and the rimmed basins of the Bay of Florida, lying in swampy terrain, will be seen here and there behind the Colorados Barrier Reef, mostly clustering toward the mainland shore. These basins have axial or radial tidal channels draining to the Gulf below sea through passes or breaches in the reef. These small, rounded and rimmed basins of the Colorados lagoon seem to be features of a present mangrove-lined shoreline like those along the north shore of Florida Bay. The writer interprets the pocket harbors of the Havana type, surrounded by a slightly elevated plain (Palmer 1945), as similar mangrove lakes scoured out at sea level in the midst of a saline swamp and then slightly elevated on the unstable young orogenic coast (Sector 3) of Cuba.

Barrier Island not an indicator of long-period sea-level change.—Johnson (1919, 1925) thought that his offshore bar, called barrier island by the writer (Price 1951a, Shepard 1952), was a feature predominantly of an emergent shoreline. He believed that the structure was formed by a semipermanent sea level change, a slight worldwide lowering of sea level or an upwarping of the crust, along an offshore bar formed originally as a submarine feature. Fenneman (1938, p. 4), following some early writers, believed, however, that a barrier island was formed merely as an equilibrium structure produced on a shallow shelving coast by the balance between wave attack and bottom resistance regardless of any history of sea level

change. The writer's study of bottom profiles in the Gulf (fig. 15) indicates that barrier islands are (1) associated with well-developed equilibrium profiles, (2) on a shallow coast where the bottom is now at least 15 to 45 feet deep within one to two miles of shore and (3) thereafter slopes outward between about 2.0 and 5.0 feet per mile, (4) where sand, gravel or cobble are abundant along shore, and (5) where onshore wave attack is strong. These observations tend to confirm Fenneman's interpretation. Other observations, briefly stated, indicate that the barrier island does not require a worldwide or other semipermanent fall of sea level to bring it above sea, but that the only change in level needed is a local, short-period change between storm levels and normal sea levels taking place during periods of a few hours or days.

A series of aerial photographs taken at intervals of several years over the period 1934 to 1949 (Bates 1953) shows that a bar formed just below the intertidal zone off a new mouth of Brazos River remained submerged until a hurricane had occurred, after which it became a typical emergent barrier island of cuspate outline. A second bar then formed off a breach in this barrier, after which other hurricanes occurred before the second bar was, in turn, raised above sea to form a second line of emergent barriers. The inference is strong that, in each case, a pre-existing submarine bar was built higher during a hurricane, so that during the storm it bore the same height relation to the elevated storm sea level as it had formerly borne to the normal level of the Gulf. The bars emerged as barrier islands after the subsidence of the temporarily high sea levels.

On October 3, 1948, a hurricane passed about 100 miles off the coast of southwestern Texas, causing a high sea level or storm tide of some 3 or 4 feet for two days or more along the barrier islands. A week later, the writer found that the summit of the beach, the beach ridge, in front of the shore dunes had been built up and remade by the storm and was slightly farther inland than its former alignment. The shift in position was evidenced by erosion of dune faces. The convexly rounded beach ridge then rested where the front part of the dunes had been.

The raising of the beach ridge, previously described, to an elevation above its position during normal times was shown by the rapid mass-wasting that had affected it in a single week. The beach ridge on this island formerly had, in places, a fairly well developed pavement of shell, but now the pavement had just begun to be formed on the newly made ridge. The pavement was formed from disseminated shell by the washing and blowing away of sand, according to a well-established process. It was evident that this ridge had lost some 6 inches of its height and would lose another foot or a foot-and-a-half before a pavement would be formed to protect it. The former paved beach ridges had evidently lost similar heights.

Reports and illustrations of hurricane damage to New England beaches (Brown 1939, Howard 1939) show that the beach ridges were remade at higher levels, moved inland from their former positions and their axes rotated slightly by the hurricane waters.

These observations indicate clearly that the summit ridge of a barrier island functions briefly during storm tides as an underwater offshore bar and thereafter emerges as a barrier island.

Evans (1942) found that waves operating at a steady sea level tend to modify the slopes and positions of underwater bars, but not to build them up above water.

The great development of active barrier islands on the Gulf coast, dominating the shorelines of the alluvial sectors (1, fig. 14), does not then, in the writer's opinion, tell a story of permanent or semipermanent sea level change, or mark either a submergent or an emergent shoreline condition.

The question of the source of the supply of material for the barrier, long thought to be a critical factor, is found to be secondary. Thus, barriers occur in the Gulf where longshore sediment drift is prominent (Sectors 1.12, 1.2, fig. 14) the sand derived largely from rivers (Bullard 1942), also where a longshore drift from a land connection (Chandeleur Islands, La.) is absent and where no land-derived sediment is present but onshore waves are strong and the barrier is built of broken shells from the adjacent bottoms, as on the north shore of Yucatán (2.2, fig. 14).

Emergent shoreline terraces and notches.—The lowest well-established elevated shoreline is that of the Pamlico of the Atlantic coast and Florida, standing at about 25 feet above mean sea level. This shoreline is marked in many regions by a well-cut and well-preserved terrace or by a broad elevated lagoon flat with a barrier island. Less

well-developed and somewhat controversial shorelines are reported from many places in the interval from about +3 to +10 feet. However, carefully selected, stable, protected, inner shoreline sectors on North Pacific Islands (Stearns 1941, 1945) and in Australia (Fairbridge 1948) exhibit shoreline cliffs in even-grained limestones with solution notches at about +3, +5 and +8 feet. These seem to represent worldwide stillstands of the sea (eustatic shorelines). Shorelines reported at +16 and +20 feet (Daly 1934 and others), are not as yet substantiated by data of unquestioned accuracy.

In places around the shores of the Gulf, there are definite indications of shoreline terraces that seem to indicate stillstands at about +5 and +8 feet. An elevated barrier island and coastal lagoon caught by the 10-foot contour has been mapped in Florida by MacNeil (1950) as the "Silver Bluff shoreline" (Parker and Cooke, 1944, pl. 4, fig. B). He did not follow it across southern Florida or on the west side of the peninsula.

Low shoreline flats appear in many places around the Gulf, but have not been critically studied in the field. Such a low bench shows in air photographs along the base of the high bluffs of the Champoton-Campeche limestone fault-block salient (fig. 12; Sector 2.2, fig. 14). It seems to have a gray, sandy soil. A flat along the front of the elevated Ingleside shoreline between the Rio Grande and Brazos–Colorado deltas (fig. 12) lying at from about 1 to about 5 feet above mean sea level has low, subdued spits and bars on its surface [15] and seems to be an emergent marine plain. It is about 0.3 mile wide. This flat may be a nondeltaic part of the original Pleistocene surface in front of this barrier. Deltaic deposits appear along the Gulf side of this barrier east of Galveston Bay.

Marsh borders the Pleistocene delta of Brazos River in Texas to an elevation of 2 to 3 feet above mean sea level. Just behind the marsh is a bench 1.0 to 1.5 mile wide at 3.0 to 4.5 feet with a low nip or wall between 4.0 and 6.5 feet above sea. This bench may be a low Silver Bluff representative.

At Buhler, a few miles northwest of Lake Charles, Louisiana, the Ingleside barrier and lagoon clays are well preserved. The top-of-clays, representing the approximate shoreline position, lies between 22 and 25 feet above sea. This shoreline and the associated features are well defined running at the same elevation from near Lake Charles west to Beaumont and thence southwest through Fannette, Jefferson County, Texas. Where the shoreline comes within about 10 miles of Anahauc, Chambers County, it is sloping down to the southwest at about 1.5 feet per mile and reaches sea level at Smith Point on the shore of Galveston Bay. Before the formation of the bay, it was formerly tied there to the Brazos delta. The Ingleside shoreline seems to correlate with the Pamlico through the emergent barrier of Gulfport and Biloxi, Mississippi.

The deltaic plain lying south of the Ingleside in southwestern Louisiana and in Jefferson and Chambers counties, Texas, is of the same age as that immediately to the north of it, Prairie or Beaumont (Hayes and Kennedy 1903, pp. 27–38; Deussen 1924, p. 110). Along the shore of Jefferson and Chambers counties, it is a partly submerged deltaic plain.

The Ingleside appears again south of the Brazos-Colorado delta along the coastal lagoon that opens from Matagorda Bay at its southeast extremity and runs from there to the north flank of Rio Grande delta, the shoreline (top of clay) being at approximately 5 to 10 feet above sea.

The disagreements in the shoreline data for the northern Gulf coast would be removed if the coast from Florida to the Mississippi delta had been stable since Pamlico time, but a slight amount of gulfward downwarping had occurred between the vicinity of Galveston Bay and the coast of Mexico at some point north of Tampico.

The post-Pleistocene gulfward downwarp of the Beaumont Pleistocene plain (Doering 1935) increases in amount from about 1 foot per mile in southeastern Texas to 2 feet per mile southwest of Matagorda Bay. This downwarp seems to mark the influence of the young orogenic coast of Mexico, which it is approaching.[16] This interpretation suggests that the emergent shoreline flat on the Gulfward flank of the Ingleside barrier may be either of Ingleside age, downwarped some 15 feet, or a younger post-warping shoreline, possibly of Silver Bluff age. Against a Recent age for the low bench is the seeming absence of marine fossils

[15] Obscured by mima (pimple) mounds higher and wider than the spits (Price 1949).

[16] Corpus Christi lies 175 miles east of folded Cretaceous rocks at the surface in Mexico and 125 miles northwest of submerged mountains in the Gulf.

above present sea level in the much cored and studied post-Pleistocene alluvial fill of Mississippi River in the Atchafalaya river basin, Louisiana (Fisk 1952).

No unquestionable evidence seems yet to have been offered that elevated, unwarped (eustatic) shorelines below +25 feet are of Recent or post-Glacial age, despite continued statements by many geologists that they "seem to be Recent." R. W. Fairbridge and E. D. Gill of Australia [17] think that the materials of the shorelines of Australia below +10 feet are not sufficiently weathered and leached to have been formed before the last major sea level lowering. On Chesapeake Bay, G. F. Carter [18] finds no post-Pleistocene deposits above a maturely developed soil, supposedly of post-Pleistocene age, which dips beneath bay sediments and has been cored into off-shore. We do not know that the shores of the Chesapeake have been downwarped. The Pamlico terrace is reported as running level along this coast from Maryland to Florida.

The only dated shoreline deposits above sea level that are thought to be of historical or earlier Recent Age of which the writer has been able to learn, come from young orogenic coasts, as that of Tripoli [19] in Lebanon (Wetzel and Haller 1945) and on the Pacific coast of South America. These coasts must be suspected of having had crustal movements going on at any time, even in recent millenia. Thus, Jerico, 175 miles southwest of Tripoli, was once destroyed by an earthquake and 200 historical shocks are reported for the area of Israel (Ball and Ball, 1953).

SHORELINE CHANGES AND PROCESSES

SHORELINE SIMPLIFICATION

Terminology.—Shepard (1937a; 1948, pp. 70–73) says that "as numerous coasts and shorelines have undergone little modification since the sea level and the land came to rest, it seemed logical to refer to these as Primary . . . and to . . . those which have been considerably modified by the waves and currents as Secondary . . ." In his tables he calls "primary" shorelines youthful and "secondary" coasts mature. Following this concept, we find that mature marine coasts have in general become simplified in contour, with their irregularities reduced by erosion, solution or sedimentation, or a combination of processes. Hence, the end result of marine action on most types of coasts is smoothing, though not always straightening, as smooth coasts may be curved.

Processes.—Simplification of a coast may consist of the reduction of projections by erosion, and the deposition of beach and other deposits in reentrants. It may also be brought about by the formation offshore in shallow water of a barrier island or barrier spits (Price 1951a, Shepard 1952). Such inorganic barriers tend to follow along a bottom contour, crossing the sites of entrenched valleys on postentrenchment fill, while the mainland shoreline is deeply indented by the shallow embayments of the former valleys. Thus, the new marine shoreline is smooth and shorter than the mainland shoreline off which it is built.

Examples.—Simplification of Gulf shorelines is shown by (1) extensive development of sandy barriers where there are or were irregularities of the mainland shoreline, chiefly between the convexities of deltas (Sector 1), (2) the gradual filling of coastal lagoons (as east of Galveston Bay, sector 1.2), (3) the incipient smoothing of projections along some sectors of the drowned karst coast (2.1), (4) seemingly some smoothing of the front of parts of the mangrove ridge (Sector 4.1) facing the Gulf, in contrast with a possibly irregular original configuration such as that of the Ten Thousand Islands or the north shore of the Bay of Florida, (5) smoothing of the karst irregularities of the elevated Champoton-Campeche fault-block (Sector 2.2, Yucatán peninsula) so that only small cuspate points remain, (6) reduction by erosion of projecting folded limestone rock (northern Sector 3.1) and of the ends of narrow tongues of lava solidified to rock extending into the Gulf from the active volcanic salients of the young orogenic coast of Mexico (southern Sector 3.1).

Significance.—The several degrees of shoreline simplification evident in the preceding list, suggest a considerable quantitative range in the effective application of marine energy to shoreline modification during the 3,000 to 5,000 years of essential stillstand of the Gulf. Just as we find variation in simplification related to the hardness and resistance of the shoreline materials, rocks or soft sediments, so we may suspect that there have been differences in the amounts of energy available

[17] Letters of 1952.

[18] Letters of 1952.

[19] At 2 to 3 meters above sea 600 m. inland and possibly 3,000 to 4,000 years old.

for shoreline work. This supposition is justified by (1) the consideration that erosion at the shoreline has a vertical as well as a horizontal component, (2) comparison of variations in the form and offshore gradients of the bottom of the continental shelf on various sectors of the Gulf, and (3) inspection of the charts of resultant winds along the shorelines of the Gulf (U. S. Weather Bureau, 1938). These factors indicate that it may be feasible, from the partly quantitative, partly qualitative data presented or referred to here, to set up a preliminary energy classification of the coasts and shorelines of the Gulf of Mexico. This is attempted in the tabulation.

Extensive Marine Modification of Coasts of Gulf.—A summary of prominent shoreline conditions that indicate the degree of coastal modification is shown in tabular form below. The simplified coasts (the secondary or mature coasts of Shepard) greatly dominate in linear distribution, indicating that the sea has been at about the same level for a substantial period of time in relation to the resistance of most of the coastal materials to shoreline modification.

	Approximate length in statute miles	*Percentage of marine shoreline length*	
Gulf and major parts:			
Marine shoreline	3,000	100	
Coastal plains	2,500	83	100
Volcanic and other sectors	500	17	
Secondary shorelines:			
Simplified (smooth)	2,250	75	100
Moderately smooth	250	8	
Little modified	500	17	
Sandy beach	1,553	52	
Barrier islands and bay barriers	1,370	46	
Inactive and elevated beach plains	810+	27+	
Beach ridges, average of 10 (?) ridges per beach	20,000+	667+	

EQUILIBRIUM PROFILE OF CONTINENTAL SHELF BOTTOM

Definitions.—Figure 15 shows bottom profiles for sectors of the continental shelf having different steepness of curvature. Only for the broad shelves off the alluvial and limestone plateau coasts (fig. 14, Sectors 1 and 2) of the Gulf of Mexico are there enough data for analysis. On the shelf sectors studied, the profile of the bottom is concave in the first mile or two, this section being the shoreface, an extension of the beach or other shore. The shoreface grades into a nearly smooth plain, here called the ramp, the gradient of which flattens slowly in an offshore direction for varying distances, commonly to 30 fathoms or more. The profiles drawn on this section of the shelf are mathematically of the hyperbolic or asymptotic type, the so-called logarithmic or exponential curves.

The ramp grades, usually far offshore, into a usually smooth convex section, here called the "camber," the gradient of which usually increases rapidly to the top of the irregular, steep, continental shelf slope. The sparse soundings available for the shelf of the young orogenic coast of Mexico (3, fig. 14), suggest that, except where a beach or barrier is present, this coast may lack a ramp, the camber beginning at or near the base of whatever shore cliff or shoreface is present. The so-called shelf break (Dietz and Menard, 1951) should be the junction between ramp and camber.

Data showing the locations and ramp slopes of the profiles (curves) of figure 15 and the sectors on which the curves are located are given in a tabulation following the illustration.

Location of profiles in figure 15.—All profiles measured perpendicular to shoreline from navigation charts U. S. Coast and Geodetic Survey.

(1) Off old Corpus Christi Pass and Padre Island barrier island 27°35′ N. Lat., 97°13′ W. Long. Chart 1286, 1922 edition. A profile at same place from original survey sheet (1880) shows only minor irregularities and smoothly asymptotic curvature to 90-foot depth. Beach. Sand and clay bottom.

(2) Off Padre Island at Baffin Bay mouth, 27°18′ and 97°20′. Chart 1286, beach sector: "Little Shell." Beach. Sand and clay bottom.

(3) Off Matagorda Peninsula barrier island, off mouth Trespalacious Bay, 28°00′, 96°10′. Chart 1284, 1945 edition. Beach. Sand and clay bottom. Fathogram off Galveston shows ramp as smooth as curves 1–3.

(4) Off barrier island on Florida peninsula 10 miles north of Cape Romano, 26°03′ and 81°48′. Chart 1254, 1931 edition. Beach. Sand inshore. Rock bottom (limestone) with some sand and shells.

(5) Off Pine Islands-Key West shoals (Miami oölite with mangrove swamp deposits above), Florida, at Johnson Keys, 24°42′, 81°36′. Chart 1251, 1940 edition. Profile begins at −8 feet. Add 8 to all depths for this curve in figure 15.

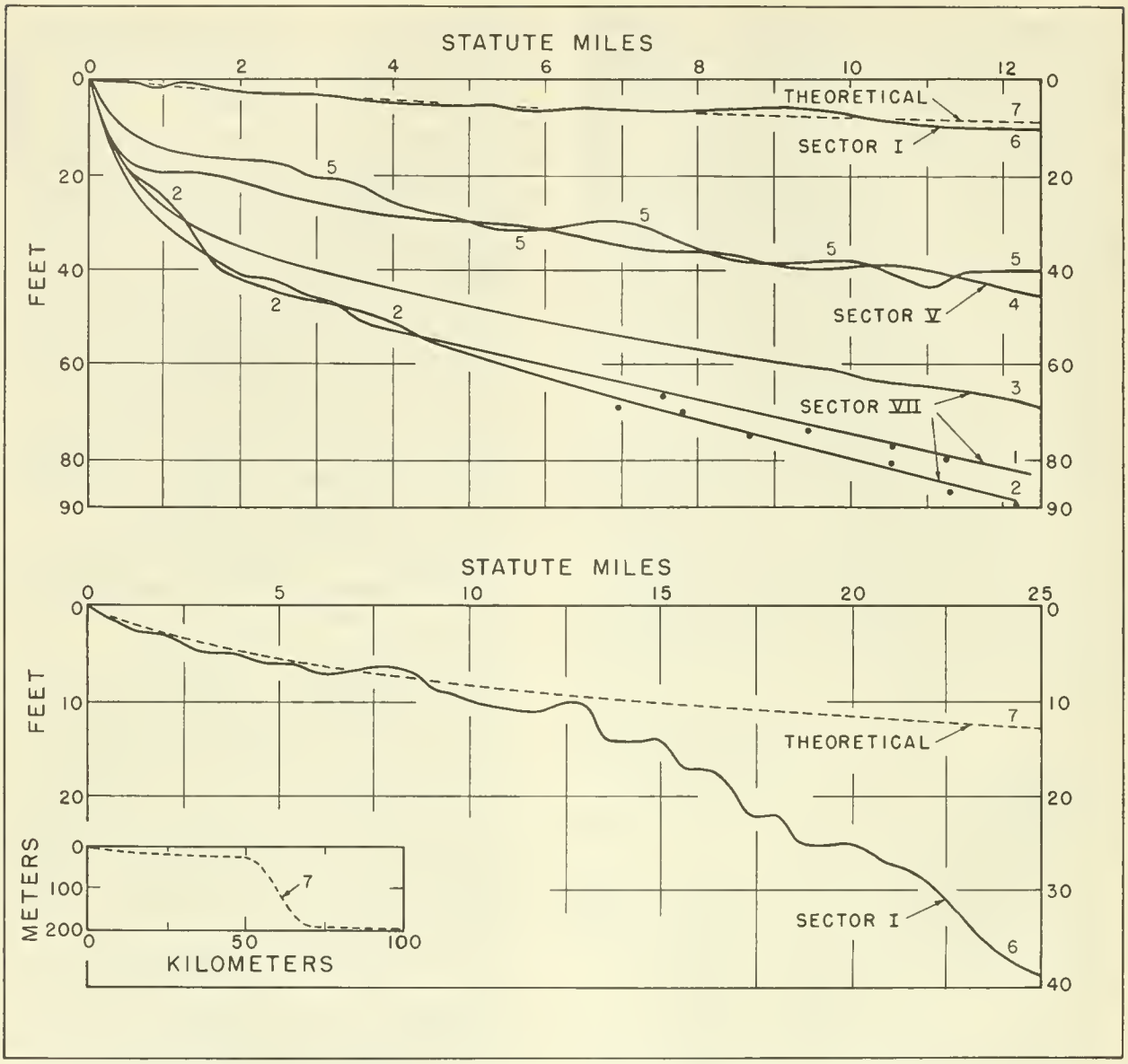

FIGURE 15.—Characteristic bottom profiles of inshore zone, continental shelf, north half, Gulf of Mexico. Steepening and progressive smoothing of bottom from profile to profile correlates with increasing energy of water, decreasing resistance of bottom, and increasing steepness of initial drowned surfaces. The theoretical low-energy, breakerless profile of Keulegan and Krumbein (curve 7) is compared with a beachless sector of drowned karst coast off Florida (curve 6). Profiles are listed on pages 59 and 60. Sectors are described in tabulation, pages 61 and 62. The shoreface extends 1 to 4 miles offshore. The ramp extends out from the shoreface as far as the profile continues to flatten. The outer parts of profiles 1 and 2 are averaged between the points shown.

Bottom "hard," mostly oölite limestone. Little sand reported in region. Beachless.

(6) Off rocky coast of Florida at Net Spread Key between Chassahowitzka and Weekiwachee Rivers, 28°38′, 82°40′. Chart 1258, 1944 edition. Beachless. Hard bottom (limestone). Very few notes of sand in region.

(7) Theoretical mathematical curve of Keulegan and Krumbein (1949) for the steepest bottom across which waves will move with the maximum height without breaking. A wave 3 m. high enters the shelf-sea on a bottom 4 m. deep 40 km. from shore. Depth equals the 4/7 power of the distance from shore. A hyperbolic curve.

TABLE 1.—*Gradients of ramp shown in figure 15*

Profile	Oradient	Statute miles from shore	Depth in feet	Sector of Gulf
7	2.0	0.1– 0.6	0.5– 1.6	Theoretical "breakerless" bottom profile, Keulegan and Krumbein.
	1.7	.6– 2.2	1.6– 3.3	
	0.6	2.2– 7.4	3.3– 6.6	
	0.4	7.4–15.0	6.6– 9.8	
	0.3	15.0–25.0	9.8–13.0	
6	1.5	0 – 4.0	1.0– 7.0	I.
	1.0	0 –13.0	1.0–10.0	
	2.0	13.0–27.0	10.0–40.0	
5	2.4	0.7–12.0	7.0–21.0	—
4	2.2	0.9–11.0	20.0–40.0	V.
3	6.0	1.0– 4.0	25.0–44.0	
	3.0	4.0– 8.5	44.0–57.0	VII.
	2.7	4.0–12.0	44.0–67.0	
2	5.0	1.8–12.2	41.0–87.0	VII.
	4.3	4.4–12.2	54.0–87.0	
1	3.5	1.8–12.2	45.0–83.0	VII.
	3.6	3.6–12.2	51.0–83.0	

Sedimentation and the profiles.—The shoreface, ramp and camber of the normal coastal plain shelf, as exhibited on the Gulf of Mexico, seem to have specific characteristics as to sedimentation (map, fig. 16, p. 79) and erosion. From meager data, it seems that sand and shifting bars characterize the shoreface. Contemporary sands, relict deltas and barriers of former sea levels, with some contemporary clay deposition, characterize the ramp. Except when the entire profile is migrating landward, transportation probably dominates the ramp after any relict elevations have been removed from the part under consideration. Fine-grained sediments, mostly land-derived clays, and presumably the process of deposition, characterize the camber. Off the mouths of large deltas, little or no coarse sand reaches the Gulf and the charts show "mud" beginning near shore. Where sand is present it usually extends to 5 to 10 fathoms (Bates 1953; Lohse 1952).

Dietz and Menard (1951) have lately advanced evidence and argument for the belief that, at the level of the passage of the shelf from the steep concavity into the gentler slope, in present terminology, where the shoreface joins the ramp, is found the depth of maximum wave action on the bottom. They term it the depth of maximum abrasion, replacing the older concept of "wave base."

If the Gulf has remained essentially at the same level for the past 3,000 to 5,000 years, as previously suggested, it is evident that, on bottoms closely approximating the hyperbolic curve the shelf bottom must be in equilibrium. This should be true especially in coastal materials of slight resistance and where large amounts of marine energy have been effectively applied. That the topography of the bottom is a simple mathematical surface with a hyperbolic bottom profile, is believed to indicate that the forces are in equilibrium. Where the bottoms are of hard rock and largely retain a subaerial topography, it may be concluded that the marine forces have inherited a surface produced under different conditions which they have been unable to destroy or to which they happen to be more or less adjusted.

The equilibrium profile of the coastal plain shelf is in a state of dynamic, not static, equilibrium. In dynamic equilibrium, variations of temporary, short-term value are to be expected. Thus, heavy storm waves are known to shift offshore bars [20] temporarily as much as a half-mile from their previous positions on the shoreface. Variation of the equilibrium will be about the mean. Marked departures from the mean are caused only by forces external to those in equilibrium. The shift of a river mouth, the coming of a lava flow, or the warping of the earth's crust, would be external forces or conditions which might upset a previously existing equilibrium on the shelf.

Usefulness of equilibrium profile.—Despite some pessimism (Kuenen 1950, p. 302) as to the value of the profile in geologic studies and much misconception on the part of writers as to the difference between static and dynamic equilibria in nature, the present writer finds that the profile of equilibrium is a suitable index of the response of a continental shelf bottom to the application of marine energy for a significant period of time. If, as some think, there have been several oscillations of sea level of as much as 10 to 20 feet during the past 4,000 years or so, a proposition that remains unproved, then the interpretation of the modification of the shorelines and shelf by marine energy is less clear than as here tentatively presented.

Theoretical breakerless curve fits Florida.—Keulegan and Krumbein (1949) made a theoretical study of the critical steepest bottom slope in shallow water on a shelf across which waves from deep oceanic waters may move but be constantly deformed and constantly lose energy so that they arrive at and near shore without enough height or energy to break or to develop shore structures, such as beaches or cliffs. The absence of such

[20] The true underwater feature, not the barrier island. This occured at Galveston, Texas.

shore structure along much of the western shores of the limestone peninsulas of Florida and Yucatán, and the low gradients prevailing there offshore, led the writer to investigate these regions for examples of the beachless and breakerless coasts. More information is available for Florida than for Yucatán.

It was found that the requisite combination of (1) unmodified or little-modified shorelines, (2) gentle offshore slope and (3) essential absence of breakers (Corps of Engineers, U. S. Army 1940) exists on long stretches (Sectors 2.1 and 4.1, fig. 14) of the Gulf shoreline of peninsular Florida.[21] By analogy, similar conditions are believed to exist on more than half the lengths of the western peninsular coasts of Florida and Yucatán, where the bottom gradient is low and the shoreline and bottom essentially unmodified by marine forces.

Comparison of the theoretical "breakerless bottom" curve of Keulegan and Krumbein (1949), described as profile 7 (p. 60 and fig. 15) with the actual rolling bottom profile of the drowned karst shelf of peninsular Florida (profile 6, fig. 15), shows that the two curves closely superimpose and are identical in over-all gradient. But the drowned karst profile has not been fully smoothed by erosion and deposition and is not yet a marine profile or equilibrium, although slight modifications of it indicate that such a development is going on.

DIRECTIONS OF LONGSHORE DRIFT

In the northwestern Gulf of Mexico, where a strong longshore sediment drift occurs, and wherever a barrier spit terminates, the dominant drift of the year is in the direction of the elongated, pointed barrier ends.[22] These criteria agree there with the known histories of inlet migration, although there is a weaker summer drift to the northeast. Using spit criteria, the dominant longshore drift is seen to be westward and southwestward, that is, counterclockwise,[23] from Apalachicola delta, Florida, to the poorly mapped volcanic sectors (Sector 3, fig. 14). Where sandy beaches and barriers occur on peninsular Florida, longshore drift occurs. A northward drift exists for 20 nautical miles from the headland at Indian Rocks (270°52′ N. Lat.) to Anclote Keys. A much stronger south-southeastward drift exists from Indian Rocks to Cape Romano and its large underwater bars, a distance of 75 nautical miles. Southeastward drift again appears south of Cape Sable, where fine-grained sediments have been carried into the northwestern part of Florida Bay. Colorados barrier reef at the western end of Cuba diverges from the shoreline to the west, suggesting a clockwise drift.[24] Split ends indicate a clockwise drift (to the west) on the north and northwest coasts of Yucatán to the Laguna de Terminos (Sector 1.11, fig. 14).

The unmodified and slightly modified drowned karst and mangrove ridge shorelines do not show appreciable longshore drift, judging by their irregular shorelines and dominantly transverse tidal channels. Convergence areas exist at the cuspate delta of the Apalachicola and the cuspate foreland of Cape Sable, Florida. The cuspate foreland of Cabo Rojo (fig. 12; Sector 3, fig. 14), is asymmetrical, showing that the counterelockwise drift persists across it despite convergence.

Bates (1953) shows from photographs and oceanographic data that there is a Coriolis effect[25] turning Mississippi River water westward along shore. This coincides in direction with a weak, westward-moving wind-powered drift. Together there is formed a dominant counterclockwise drift (to the right). Distribution of sediments along the delta front agrees well with this drift. Air photographs show that the Coriolis drift occurs also at the mouths of the other rivers of the northwestern Gulf coast. It is not operative, however, in equatorial and near-equatorial waters such as the southern Gulf of Mexico.

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[21] The data on waves and swell are being studied at the Agricultural and Mechanical College of Texas by Charles Bretschneider (Bretschneider and Reid 1953).

[22] The so-called Gulliver's rule (Johnson 1919, p. 376) cannot be applied here successfully in all cases from chart data and is of doubtful validity in any case. See Bullard (1942) and Price (1952).

[23] With reference to the center of the Gulf.

[24] Observations of drift in this direction have been recorded. The drift seems to be powered by a clockwise eddy developing off the right flank of the Yucatán current (N. to NNE. through Yucatán Channel; Leipper p. 121, fig. 34).

[25] Relative right hand turning of flows because of the rotating coordinates of the revolving earth. The turn is to the left in the southern hemisphere.

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GEOLOGY OF THE GULF OF MEXICO [1]

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The lower Gulf coast and the inner continental shelf of the Gulf of Mexico are the sites of oil fields in Veracruz, Tamaulipas, Texas, Louisiana, and Florida. Therefore, hundreds of geologists, geophysicists, and engineers are engaged in investigations of the structure, geologic history, and sedimentology of the fringe of the Gulf of Mexico. Due to the economic necessity for research to discover new trends and new provinces of petroleum accumulation and to the many data continuously being furnished by the drill and geophysics, great strides have been made in the knowledge of the continental shelf and the adjacent Coastal Plain of the United States. Even though these economic studies were of the coastal area and continental shelf, they have encouraged thought concerning the origin and geologic history of the Gulf of Mexico.

A modern study of the Gulf Stream was initiated by the United States Coast Survey in 1846, and some work in the Gulf of Mexico was started soon thereafter. During the last century, many capable students of geology have studied the geological history of the Gulf of Mexico, but there is still much diversity of opinion concerning its origin and manner of development.

EARLY CONCEPTS

Early European writers initiated the idea of North and South America being tied together by a continuous mountain system, and this century-old concept is still popular in Europe. Suess (1885, pp. 283–285) described the Gulf of Mexico bottom as an elevated "plate" and considered this plate the foreland of the Antillean chain. He believed the present deep Gulf did not exist in Paleozoic time, but an old metamorphosed and deformed basement formed a somewhat flat platform that continued southward the low-lying central area of the United States. The present Gulf of Mexico was formed by the collapse of the plate during Cretaceous and later time, and the general outline of the Gulf was "not influenced by the course of the mountainfolds unless perhaps in the west by the approach of the Mexican ranges to the coast of Vera Cruz" (1885, p. 551). The plate of Suess has influenced geologic thought concerning the origin of the Gulf for the past three-score years.

Spencer (1895, pp. 103–140) not only believed that the whole tract of the Caribbean Sea, the Antilles, and the Gulf of Mexico constituted an ancient continental region, but he attempted to restore the topography of the submerged continent. Using available soundings, Spencer found drowned valleys which he considered of prime importance in establishing the existence of a continental region which ever since the Miocene had executed vertical fluctuations of an amplitude of many thousands of meters. In discussing the area, he stated, "the Gulf of Mexico appears to have been a plain, with the fjords and embayments reaching nearly to its greatest depths" (1895, p. 119). Thus, Spencer agreed with Suess, at least in part, and postulated a Gulf floor more than 12,000 feet above its present deepest position.

Hill (1898, pp. 3–5) believed the Gulf of Mexico is more closely related to North America than to Central or South America. He declined to consider most of the Antilles as other than true oceanic formations and refused to believe that there is any connection between the northern Antilles and Barbados-Trinidad, the latter being by him assigned to the South American mainland. He saw that the Gulf is nearly surrounded by low plains composed of nearly horizontal, unconsolidated sediments deposited in an enlarged Gulf of Mexico. This border of plains is in direct contrast to the Caribbean and its mountainous periphery.

Willis (1929, p. 328) held that basins are permanent, and he did not believe the Gulf of Mexico

[1] Contribution from the Department of Geology of the Agricultural and Mechanical College of Texas, Oceanographic Series No. 18.

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was ever an area of shallow seas over a flat "plate." This is shown by his statement that

> The isostatic equilibrium of the Gulf is inconsistent with the conditions that should result if a continental mass had sunk . . . I, myself, regard the Gulf as representing a mass of basalt which was erupted in Pre-Cambrian time, either before or soon after the eruptions of the granitic nuclei of North America. If so, it has been a basin ever since . . . The Caribbean, Yucatan Deep, and the Gulf of Mexico are, from the point of view of actual isostatic equilibrium, all of the same nature. They are, I think, all of them basins of great antiquity.

Van der Gracht (1931, p. 121) discussed the origin of the Gulf of Mexico and the downbreaking of Llanoria. He believed the coastal plain "represents a sunken basin over old central chains" and that both the Caribbean Sea and the Gulf of Mexico were part of a great geosyncline and a "very complicated system of anticlinoria, ridges and chains . . . must now fill the original geosyncline, generated by its late-Paleozoic compression stage. Since then, complete abrasion and renewed sedimentation . . . have obscured the original structure."

Fifty years after Suess, Schuchert (1935, p. 340) confirmed the conclusion of Suess as to the Gulf of Mexico "plate" and described it as extending from Tabasco northward so as to include part of Texas, Arkansas, the southern tip of Illinois, Alabama, the peninsula of Florida, and the northern Bahama Banks, as well as other Mississippi embayment States.

The Gulf of Mexico and the Caribbean were separated, according to Schuchert, by a Central American-Antillean anticlinorium until Jurassic time. By mid-Cretaceous, the Gulf of Mexico area responded to crustal movements in Mexico and the Antillean geanticline and began to subside; this downward movement continued until great depths were reached. Thus, the Gulf of Mexico was a shallow sea probably from Proterozoic to mid-Mesozoic time, and by late Cenozoic time the depth had changed from possibly less than 1,000 to over 12,000 feet. Schuchert believed the cause of the inbreaking of the "plate" and the subsequent subsidence was related to "the geologic structures of the Central American-Antillean region, those of northern South America, and those of the present Caribbean sea bottom" and that all were "due to subcrustal flowage, to the rising of plutonic masses into the various arches, and to the subsequent cooling of these masses." He also believed that—

> The present depth of 12,000 feet was surely exceeded during Cenozoic time, since in the course of this era sediments thought to be many thousands of feet thick accumulated upon it . . . In the latitude of South Louisiana, the ancient Gulf bottom has subsided over 25,000 feet, about twice the depth of the present Mexican Basin (Sigsbee Deep). Therefore we may say that the greater part of the Gulf of Mexico has sunk since Middle Cretaceous time at least 20,000 feet. These are striking facts, indicating slow, but in the end enormous, loading and isostatic adjustment, accompanied by subcrustal movements and rock flowage toward the rising geanticlines of Mexico and the Central American-Antillean arch, a movement that is not yet completed.

GULF COAST GEOSYNCLINE

Barton, Ritz, and Hickey (1933, pp. 1446–1458) were among the first to publish concerning the Gulf coast geosyncline, and they presented both stratigraphic and geophysical evidence for the existence of a geosyncline in the Gulf coast of Texas and Louisiana. They showed geophysical calculations to indicate a horizontal increase in density of the basement rocks from the Sabine uplift to near the middle of the Gulf of Mexico, and they concluded that a geosyncline must occur in the basement surface with its trough axes slightly landward from the present coast line (op. cit., p. 1456). They also showed the great thickening of the Upper Cretaceous and Tertiary beds as they dip Gulfward, with the Tertiary beds reaching a stratigraphic thickness of more than 25,000 feet near the coast. Knowing that the deepest part of the Gulf of Mexico is 12,500 feet and assuming that the thickness of the Upper Cretaceous–Tertiary sedimentary deposits in the great depths of the Gulf are 10 percent or less of their thickness in the Gulf coast, it was concluded that "the basement of the Upper Cretaceous–Tertiary beds must be down-warped 6,000 to 16,000 feet in reference to the depth of that basement under the Sigsbee Deep."

The geosynclinal trough is a well-marked feature indicating considerable subsidence. Its westward limit is not definitely known, but some thinning of formations is noted in the longitude of Matagorda County, Texas. It is further complicated by transverse structures such as the Rio Grande syncline, the San Marcos arch, the Houston syncline, the Sabine uplift, and the Mississippi River syncline.

Howe (1936, p. 82) called attention to the great sinking in the region of the Mississippi Delta which he believed amounted to about 30,000 feet since the beginning of the Tertiary. He believed the Gulf coast is an active geosyncline resulting from the weight of the sediments brought down by the Mississippi River. Evidence of the sinking of the Mississippi Delta was also presented by Russell (1936, pp. 167–169) in his study of the physiography of the region. Russell and Fisk (1942, pp. 56–59) questioned the "strength" of the earth's crust and concluded that the crust appeared "weak" as it yielded and subsided "at essentially the same rate that the deposits thickened."

Meyer (1939, p. 206) did not subscribe to the sedimentary-load theory and among various objections stated that the "epochs of reversal of movement in the geosyncline, indicated by unconformities, shoreline migrations, entrenched streams, submarine canyons, and the elevated beach at Corpus Christi, are opposed to the basic tenets of the sedimentary-load theory."

Meyer also used the argument that the ocean deeps, which are structural troughs, could not have been caused by the weight of accumulating sediments. He suggested that the Mexican Basin and the Gulf coast geosyncline may be related structures and that the Gulf coast geosyncline was a "similar structural and topographic basin in early Tertiary time when the strand-line was far inland. After this basin had come into existence, it offered an opportunity for the accumulation of thousands of feet of sediments. The weight of the first several thousand feet of Tertiary deposits may have been sufficient to overcome the inherent strength of the crust and to cause further sinking" (op. cit., p. 206).

Storm (1945, p. 1330) considered the Gulf coast geosynclinal trough as a well-marked feature indicating considerable subsidence. He believed that, if subsidence continued at a fixed position and if sediment filled this trough and passed over it, there should be some sign of sinking inland and drainage should have caused deposition over the axis of the syncline. Such indications were lacking, and he therefore believed that the shape of the trough was a composite of past and present. He showed that sediments are accumulating principally on the seaward flank of the trough which pushes the bottom of the flank downward while the landward flank rises slightly. Thus, the trough tends to move seaward with continued sedimentation.

Glaessner and Teichert (1947, p. 586) thoroughly reviewed the subject of geosynclines and concluded that the origin of geosynclines is still unknown. Observed facts are too often overshadowed by an author's "attitude to one or the other of the current and mutually exclusive hypotheses of mountain building and of the origin of continents on which no finality has yet been reached. Concerning the actual mechanism of the formation of geosynclines it would seem that the school of Gulf coast geologists has produced such weighty arguments in favor of subsidence under load that the operation of the factor can no longer be doubted. On the other hand, there is evidence for 'autonomous' uplift and subsidence of parts of the crust which would make it possible for sedimentary accumulations to be formed as a result of active subsidence and uplift rather than of passive depression under the load of shifting products of erosion."

Bornhauser (1947, pp. 706–711) observed that, since the Tertiary transgressions affected the whole northern border of the Gulf of Mexico, diastrophic movements must have been the primary cause of the transgressions. He agreed that the subsidence of the Mississippi embayment and the Gulf coast geosyncline caused the Tertiary transgressions of those areas, and the subsidence was due to diastrophic movements. Bornhauser "has not found clear evidence to support the idea that the weight of the sedimentary column is the deciding factor for subsidence. On the contrary, all facts and evidences seem to point toward the conclusion that the formation of the Mississippi embayment is a tectonic incident closely related to the structural history of the Gulf of Mexico which underwent considerable epeirogenic movements during the Tertiary."

The idea of a Gulf of Mexico neutral plate was introduced by Suess and substantiated by Schuchert who considered it to be the foreland of the Antilles. Bornhauser accepted this neutral plate and suggested that the northern border of the plate may have formed the submarine plateau of southeast Mississippi, at least during earlier Tertiary. Deeper synclines separated this plateau

from the land masses on the northwest and north, particularly during Midway-Wilcox time.

Bornhauser (op. cit., p. 709) stated:

> In order to explain the progressive enlargement of the southeast Mississippi plateau and the corresponding shifting toward the north and northwest of its frontal synclinal zones during the Eocene, the theory is advanced that this plateau, together with the Gulf of Mexico "plate," drifted in successive stages to the north as a result of Tertiary orogenic movements in the Antilles. A maximum penetration of the plateau into the Mississippi embayment was reached at the close of the Eocene and early Oligocene periods, when it touched the northern land masses. A breakdown of the southern part of this plateau and a large part of the Gulf of Mexico followed during the Oligocene and Miocene, forming the present Gulf of Mexico. This downbreaking in connection with the emergence of the embayment probably caused a change in direction of the Gulf Coast geosyncline in south Louisiana. During the Eocene, the axis of this syncline followed a southwest-northeast trend, with the Mississippi embayment syncline forming its northeastern extension. With the formation of the present Gulf of Mexico during Oligocene and Miocene time, this axis was diverted to a west-east trend.

Trask, Phleger, and Stetson (1947, pp. 460–461) obtained sediments from the northwestern part of the Gulf of Mexico during the 1946 expedition of the *Atlantis*. In the central part of the Gulf, where the depth of water exceeds 11,000 feet, two distinctly different layers of sediment were found. A thin top zone of globigerina was underlain, in most cores, abruptly, by alternating clay and very fine, well-sorted silt containing a cold water fauna. In other cores, from the same depth, ripple marks and crossbedding were found. Such conditions suggest shallow-water deposition; and, to get such conditions, it is necessary to assume either a rather recent great depressing of the Gulf floor or an equally great lowering of sea level. The other alternate is to assume sufficient currents at depth to cause sorting, ripple marks, and crossbedding.

Lowman (1949, pp. 1986–1993) believed that the central part of the Gulf of Mexico might have been epicontinental in character during Eocene time. The evidence cited includes the wide extent of the Eocene into the transverse embayments, the gentle depositional slopes, the dominance of continental shelf faunas, and the character of the sediments of the southeast Mississippi platform. In contrast to the Eocene, the Upper Tertiary is absent from the transverse embayments and has continental-slope facies on relatively steep depositional slopes. Therefore, the Upper Tertiary supports a deep hole in the central part of the Gulf of Mexico, as it is today, though not necessarily in the same location.

Lowman did not believe the stratigraphic evidence was conclusive that the Mississippi River syncline subsided in response to load. He believed some workers have used facies criteria instead of planes of stratification in the isopach maps which find "maxima under the delta in the Quaternary and the Pliocene-Miocene" (op. cit., p. 1991).

Weaver (1950, p. 359) studied the continental shelves of the Gulf of Mexico and decided that a significant tectonic zone is at the outer edge of the continental shelf. He concluded that the topographic contours on the continental slope are really structural contours and that they exist in sufficient number to indicate active tectonic regional features. He proposed "the theory that the Gulf of Mexico as a deep sea is young, and that its present central great depth is due to downfaulting." The most intense faulting is indicated along the outer margin of the continental shelf west of Florida and near Yucatán, but even the more gentle continental slopes are considered fault zones. No definite time of faulting was given by Weaver.

Moody (1950) favored a single salt mass as the source of the Gulf coast and Mexican domes and suggested that it may extend across the Gulf of Mexico into the Isthmus of Tehuantepec. If this is true, the Gulf of Mexico was shallow enough to allow salt deposition beyond the present continent during the time of the deposition of the Eagle Mills salt, which is Jurassic in the opinion of Moody, although some writers place it in the Triassic or Permian. He believed the Gulf of Mexico had some downwarping during Upper Cretaceous; that it began to take shape at the end of the Laramide Revolution; and that it subsided, and maybe formed the Mexican Basin, in post-Reynosa (Pliocene) diastrophic movements. The finding of Reynosa gravels in Florida at an elevation of 360 feet suggests a great change in sea level to allow these gravels to be transported there. This means a great post-Reynosa diastrophic movement during which the west Florida shelf scarp and possibly the Mexican Basin came into existence.

Eardley (1951b, p. 2236) stated that "the Gulf of Mexico came into existence after the Appalachian orogeny by subsidence." Much of the Gulf is surrounded by the belt of late Paleozoic orogeny,

and sediments dating back to at least the Permian are found in its marginal areas. Eardley believed that the margins of the Gulf have had a near balance between subsidence and deposition, while subsidence has exceeded deposition in the central Mexican Basin.

King (1951, p. 175) stated his belief that the origin of the Gulf coast geosyncline was uncertain, but he believed "that the geosyncline represents an independent tectonic feature and perhaps a new mobile belt in its early stage of development."

The theory of Weaver that fault scarps bound the present central great deep of the Gulf received additional support by Jordan (1951, p. 1991) who described the escarpment off the panhandle of Florida. This escarpment occurs in 700 to 900 fathoms of water, and the sea floor is offset 6,000 feet or more in some places. Comments on Jordan's paper by Stetson (1951, p. 1993) confirmed the findings of Jordan and noted that the escarpment maintains about the same height and slope southward along the west Florida shelf. Stetson further commented that "from the overall picture of the whole area, one gets the impression that the bottom of the Gulf has foundered and that at least this continental slope is due to a normal fault" (idem.).

To date little exploration in the Gulf of Mexico has had as its objective the determination of major tectonic features. The cost of marine geophysical surveying and the drilling of offshore wells are such that the tectonics of the Gulf must be approached indirectly by using soundings and bottom samples together with observations of the shore features.

GEOMORPHOLOGY OF GULF OF MEXICO

The topography of the Gulf of Mexico is too scantily mapped to show the degree of development of the different types of topography so far known there.

As early as 1878 Agassiz (1878–79, p. 1) noted two of the striking topographic features of the Gulf, the great limestone banks: one west of Florida and the other northward from the peninsula of Yucatán. In both cases the 100-fathom line is somewhat parallel to the shore and forms the inner edge of the steep slopes descending to the Mexican Basin, which is another major feature of the Gulf. The varying development of continental shelves and the irregular continental slope with its escarpments, basins, knobs, and troughs are also striking features of the Gulf of Mexico.

GENERAL CHARACTERISTICS

The continental shelf forms an almost continuous terrace around the margin of the Gulf of Mexico. The major breaks occur in the Straits of Florida and the Yucatán Channel which form outlets from the Gulf to the Atlantic Ocean and Caribbean Sea, respectively.

The shelf is not an expressionless plain lacking in interesting physiographic features as may be suggested by some maps with a contour interval too great to properly present the smaller features. This terrace or shelf has numerous depressions, troughs, ridges, minor knobs, coral heads, escarpments, and two known submarine canyons.

The widest parts of the continental shelf in the Gulf of Mexico lie off Texas and the peninsulas of Yucatán and Florida. The shelf width varies from 8 to 117 miles in the northern Gulf, the maximum width being off western Florida. Other shelf widths include: 40 miles off the southern tip of Florida, 52 miles off the Isles of Dernieres, Louisiana, 110 miles off the Sabine River mouth, 40 miles off the Rio Grande outlet, and 135 miles off western and northern Yucatán.

The continental slope differs from place to place not only in width and steepness but also in physiographic features associated with it. The continental slope, in general, constitutes one of the great relief features of the earth. The edge of the continental shelf is only very roughly parallel to the shore line as is shown by the varying width of the shelf. The continental slope varies greatly in width with a minimum width west of Florida and west and northwest of the Yucatán Peninsula.

ORIGIN OF MAJOR FEATURES

The continental shelves of the Gulf of Mexico seem to have a close geologic and physiographic relationship with the adjacent land. Broad shelves lie in front of broad coastal plains, and narrow shelves lie between steep continental slopes and rugged near-shore terrain.

There is no simple explanation of the origin of the shelves and slopes, or of some of the features of these provinces, that has gained wide acceptance.

In discussing continental shelves, Pratt (1947, p. 661) observed that "modern investigations have also confirmed Nansen's pioneer observation that the inland portion of the continental shelf is a surface of degradation." Umbgrove (1946, p. 249) stated, "it appears that the history of the shelf was rather complicated. Sedimentation, abrasion, and denudation played their role. The area was subjected to changes of sea-level and movements of the bottom. Wind-waves and tidal currents acted upon the sediments of the shelf. The influence of each of these and still more factors in the building of the submerged part of the continental margin is still an open question." He also believed that the landward part of the shelf may have resulted from planation when the sea was some 300 feet lower than at present.

Many workers believed that the topography of the shelves resulted from subaerial erosion. Dana (1863, p. 441) stated this was accomplished by the elevating of the land. Long coast lines would have to be uniformly elevated to such heights that most geologists agree the hypothesis has too many difficulties to be acceptable. The lowering of sea level could also produce conditions for subaerial erosion. Shepard and Emery (1941, p. 154) found that the formation of Pleistocene ice could account for lowering sea level 2,200 feet; Veatch and Smith (1939, p. 41) believed sea level was lowered 12,000 feet and restored in the last 25,000 years; Fisk (1944, p. 68) found evidence for a drop of sea level of 400 to 450 feet; and Carsey (1950, p. 375) suggested that if sea level was lowered 420 to 480 feet "the origin of the shelves could be attributed largely to wave planation."

The irregularities of the bottom of the shelves and the great valley-like notches along the outward slopes of the shelves are also unsolved problems. Umbgrove (1946, p. 249) believed "the phenomena of the continental margin are correlated with other periodic events occurring in the earth's crust and its substratum."

Daly (1936, p. 401) introduced the idea of density currents or "bottom streams of sea water containing mud in suspension and therefore temporarily endowed with density greater than that normal to the clean water overlying the respective continental terraces. It is further supposed that the conditions for the formation of such bottom currents were specially developed at certain stages of the Glacial Period . . ." This heavy mass of mud and water would naturally move into the depressions on the continental shelf, and in places it would flow over the margin of the shelf and down the continental slope with accelerated motion and force.

A new hypothesis for the origin of continental slopes and submarine canyons has been suggested by Emery (1950, pp. 102–104). He proposed that "thrusting along a shear plane at the continental margins may result in a temporary upbulging of the margins above sea level. During the time of exposure erosion by streams should have incised canyons which now, after isostatic readjustment of the margins, constitute the widely distributed submarine canyons. Known downwarped peneplains below the surface of continental shelves may have been developed on the bulged margins by long-continued erosion. The margins may, thus, have served as sources of some sediments now found on land and believed to have been derived from a seaward direction."

Kuenen (1950, p. 497) adhered to the belief that "the action of turbidity currents, especially during the ice ages" cut the submarine canyons along the edge of the shelf and slope of the continents.

An examination of the maps of the topography of the outer shelf and slope of the northern Gulf of Mexico shows many features which suggest an origin due to density currents and the deposition of the mass of mud. Also, continental shelf fauna dredged from the Mexican Basin may have been transported from the shelf by turbidity currents. Furthermore, these currents may have carried sediment to the central Gulf and, therefore, aided in developing the rather flat floor of the Mexican Basin.

GEOMORPHOLOGY BY AREAS

Soundings in only a few areas of the Gulf are adequate to permit the drawing of accurate maps of the surface of the continental slope. More information is available concerning the northern Gulf; therefore, this area is discussed in some detail starting with the Straits of Florida and progressing in a counterclockwise direction.

EASTERN GULF AREA

The Florida Plateau includes not only the State of Florida but an equally great or greater area that lies submerged beneath water less than 50 fathoms deep and forms the Florida shelf (H. Gunter, 1929, p. 41). This plateau has been in existence since ancient time and is a part of the Gulf of Mexico "plate" of Suess and Schuchert. Its history includes submergence during Upper Cretaceous, part of Oligocene, and Upper Miocene. Since Miocene time uplift has continued, and erosion has removed much of the once continuous cover of Miocene sandy limestone. The Florida Peninsula now has very little relief. It has a wide continental shelf off its west coast, thus demonstrating the physiographic similarity between the coastal plain and the adjacent continental shelf.

The 1947 expedition of the United States Coast and Geodetic Survey ship *Hydrographer* in the waters on the continental slope southwest of the Apalachicola River, Florida, has been reported, in part, by Jordan (1951, pp. 1978–1993). Many new and interesting data have been secured in the 25,000-square-mile area of this report.

The greater part of the continental shelf west of the peninsula of Florida is covered by about 40 fathoms of water, and the slope out to the 100-fathom contour is for the most part gradual. The westward slope varies from 1° at the north to 5° at the south end of the shelf.

In the 25- to 80-fathom depths, domes, ridges, and troughs were discovered; escarpments and knobs with a relief of more than 300 feet were found in the 70- to 90-fathom depths. Most of these features occur along the shelf margin.

Within the 400- to 1,760-fathom zone the continental slope contains a deep escarpment, faults, and the terminus of the De Soto Canyon, as well as domes and depressed areas.

The continental slope escarpment is of special interest since it may materially aid in the ultimate solution of the origin of the Gulf of Mexico. Jordan (op. cit., p. 1991) noted a 35° gradient on a 4,000-foot drop, contrasting with 1° gradients or less above and below the escarpment. A ridge 30 miles long parallels the escarpment at 700 to 800 fathoms, and ridges and troughs with relief up to 600 feet occur along the bottom of the escarpment. The main escarpment undoubtedly represents faulting, and some of the minor troughs and ridges may have a like origin.

There can be little doubt that the Florida Plateau has been faulted along its western edge, but the faulting is difficult to date. Schuchert believed this faulting was due to the inbreaking of the Gulf of Mexico "plate" and that it probably began in the Upper Cretaceous. However, Weaver (1950, p. 359) believed "that the Gulf of Mexico as a deep sea is young" and therefore the faulting must have occurred at a much more recent date.

MISSISSIPPI DELTA AREA

The Mississippi River brings to its mouth a daily load of sediment in the order of 2 million tons. This material has permitted the Mississippi to build its delta out on the continental shelf with the overlapping delta reaching within some 10 miles of the landward edge of the continental slope. It might be expected that a deep trough would exist in the outer edge of the continental shelf in front of the Mississippi River, but such is not the case.

An ancient, deeply buried channel is found about 30 miles southwest of the passes of the Mississippi River. Shepard (1948, p. 213) stated that this trough, which has a depth of 1,800 feet, is the only major indentation in the shelf margin in the Gulf of Mexico and that the trough-head penetrates the shelf for nearly 30 miles. The sides are steep, and the flat floor is filled with loosely consolidated sediments. The canyon has been traced out on the continental slope to a depth of 900 fathoms before it becomes merged in the irregularities of the slope.

A second trough, called De Soto Canyon, has been discovered off the Apalachicola River of southwestern Florida. Shepard (1948, p. 179, fig. 65) reproduced a map of this trough or canyon as contoured by H. W. Murray of the United States Coast and Geodetic Survey. This map shows a series of depressions, some with relief exceeding 20 fathoms, along the bottom of the trough and a few depressions along the sides of the trough. This canyon is shown in Jordan's map (1951, p. 1982, fig. 2) of the continental slope. The canyon has a relief of about 600 feet, heads near the 240-fathom contour, and terminates near the 500-fathom contour. Stetson (1951, p. 1993) stated that cores of the steepest walls of the canyon showed sediment and no bed rock.

Upwellings of clay, locally known as mudlumps, occur near the mouths of the Mississippi River passes and have never been reported from any other delta. These mudlumps have been the subject of written discussion for more than a century, but only a few writers have attempted a scientific explanation of them. The most recent study has been made by Morgan (1951) in conjunction with the Corps of Engineers at New Orleans.

Mudlumps and mudlump islands have attracted much attention since they may have mud cliffs with a relief of up to 10 feet in an area where the average relief is usually 2 feet or less.

Most mudlumps have central cores of fine-grained plastic clay surrounded and sometimes capped by irregularly stratified layers of clay and silt. The upwelling of the clay core usually produces fissures and faults with vertical displacements resulting in central grabens. The stratified layers dip away from the islands, often forming doubly plunging anticlinal structures. Local cones along the faults and fissures are formed by the discharge of mud, gas, and salt water.

Morgan (ibid.) believed that the "formation of new lumps and rejuvenation of old lumps occurs as a direct result of excessive sedimentation at the river mouths" and "the deforming force which caused mudlump uplift is the static pressure of the sedimentary mass continually being dumped beyond the mouths of the passes."

NORTHERN GULF OF MEXICO

The continental shelf off Louisiana and Texas is somewhat uniform and has a gentle slope to about the 50-fathom contour. From this point the slope increases to the 70-fathom line where it has an increase in gradient to the 100-fathom depth. Some increase in slope is noted beyond the 100-fathom line, but the bottom becomes so irregular that the true slope becomes obscure.

Probably the chief characteristic of the continental slope of the northern Gulf is the hummocky topography. Shepard (1937, p. 1350) found 26 topographic features off the coast of Louisiana some of which had a relief of several hundred feet. Charts revealed that the belt of domes can be traced definitely for 180 miles west and southwest of the Mississippi submarine trough. More recent data show that some of the depressions are 2,000 feet deep, and some of the hills have a relief of at least 2,500 feet.

Carsey (1950, p. 376) found 164 topographic features along the shelf off the coast of Louisiana and Texas. An area of apparent concentration of these features is shown in figure 16. However, it is probable that there are many somewhat similar features elsewhere on the continental shelf and slope. They seem to be most prevalent in the area between the 100- and 750-fathom contours.

It is particularly interesting to note that no stream patterns have been found other than the troughs on the margins of the slope off the Mississippi Delta and the Apalachicola River (Shepard 1948, p. 178).

Price (1951, p. 32) observed that the "rugged topography of the northwestern shelf-margin or slope seems to contain dislocated segments of submarine canyons" which differ in late history from the canyons along the less rugged slope to the east. This suggests that the front edge of the shelf was faulted down in slices as it was built out into the Gulf.

Available maps of the topography of the Gulf bottom vary widely in their representation of the physiographic features. The amount of time as well as the number of soundings available influence the choice of the contour interval. Thus, the Treadwell (1949) map of the continental slope of the northwestern Gulf of Mexico, contour interval of 50 fathoms, shows a great number of closed basins and knobs between 91° and 95° W. Long. and 27° to 28° N. Lat. Also, there are suggestions of drainage patterns that are not evident in the map by Shepard (1948, p. 178, fig. 64) with a contour interval of 100 fathoms. Some of these differences may be due to the contour interval, but some may also be the result of additional data and the choice of the cartographer when more than one interpretation of the data exists.

All available maps of the continental slope of this region show the same general characteristics of the Gulf bottom: a very irregular, hummocky, knob and basin topography.

Minor near-shore features of ridge and trough were noted by Kindle (1936, pp. 866–867) along the Louisiana coast. He waded across a 1,500-foot traverse and found ridges whose crests were 10 feet wide and separated by troughs from 60 to 90 feet wide. The same traverse was repeated

2 days later, and while the ridges were free of mud, the depressions were filled with several inches of mud. Therefore, the whole character of the local bottom was changed in 48 hours. This shows the futility of making sweeping conclusions from only a few data, especially in the shore zone.

MEXICO

Too few data are available on the topography adjacent to Mexico to make a detailed study of either the continental shelf or slope of this region. However, some generalizations may be made from the scanty sounding data and geological maps of the adjacent land.

Mountain ranges, trending northeast-southwest, have been mapped 90 and 110 miles east of the mouth of the Rio Grande. The range nearer the coast has a known relief of 2,750 feet with a summit reached at a depth of 540 fathoms and the other range has a known relief of 3,810 feet with a summit at a depth of 839 fathoms.

Due east of Tampico a mountain range, with a bearing of N. 65°–70° E., extends some 40 miles and has a relief of 5,800 feet with a summit rising to within 33 feet of the surface.

Along the extreme western edge of the Gulf of Mexico, south of Tampico, the continental shelf is narrow, and the adjacent coastal plain is also narrow, being locally practically absent. Tertiary and later igneous rocks occur in the Misantla-Japala area, northwest of Veracruz, and in the Alvarado-El Paso area, south of Veracruz. Some of the highest peaks of Mexico occur just northwest of Veracruz. Lava flows cover much of the near-shore land area and locally form 1,000-foot cliffs at or very near the shore. South of Veracruz other smaller cones are very near the coast. While local narrow beaches are formed and break the surface continuity of igneous rocks, undoubtedly the offshore irregular topography is due to underwater outcropping of these igneous rocks.

Practically all of the Yucatán Peninsula forms a broad coastal plain. This peninsula tilts northwestward and passes under the Gulf to form a continental shelf averaging over 125 miles in width. The shelf terminates abruptly to the west and north, and the topographic contours along its edge are undoubtedly also structural contours and represent faulting.

MEXICAN BASIN

There is within the Gulf of Mexico, but not centrally situated, a large triangular area with deeps exceeding 2,000 fathoms. It lies northwest of the Campeche Banks approximately between 22° and 25° N. Lat. and 89° and 95° W. Long. Regarding this area, Hilgard is quoted by Agassiz (1888, p. 101) as follows: "The large submarine plateau below the depth of 12,000 feet has received the name of the 'Sigsbee Deep', in honour of its discoverer." Since the "depth of the basin does not attain 3,000 fathoms, it is not a 'deep' in the Murray sense, but it is an enclosed, distinctive basin, for which Sigsbee's name may appropriately be retained" (Vaughan 1940, p. 66).

More recently, however, the name "Sigsbee Deep" has been restricted to the deepest measurement in the basin, and the name "Mexican Basin" is used here for the broad, enclosed basin.

The bottom of the Mexican Basin is very flat, especially when contrasted with the continental slope of the Gulf. The depths range from 2,000 to 2,070 fathoms over the deepest part of the basin. The bottom rises rather uniformly to the shore in the west in a distance of 180 miles, but the northern slope is more gentle and apparently more irregular in its distance of 300 miles. The slopes toward Florida and the Yucatán Peninsula are broken by abrupt changes which undoubtedly represent faults in the bottom.

One of the most prominent mounds in the Gulf is found in the northeast portion of the Mexican Basin. It has a relief exceeding 890 fathoms, a possible width of 60 miles, and its top is encountered at a depth of 916 fathoms.

SEDIMENTS OF GULF OF MEXICO

SOURCE OF SEDIMENTS

The near-shore sediments, at least, should be expected to be closely related to the sediments of the adjacent coastal plain except near the mouths of major rivers. Much study has been given samples obtained from wells and outcrops in the area surrounding the Gulf of Mexico. Such studies have shown that each formation varies widely in its composition as it curves around the Gulf from Florida to Mexico.

The Tertiary outcrops in the Gulf Coastal Plain include thick continental sandy and lignitic deposits and thinner marine sands and clays. Down-dip from the outcrops, drilling has shown that the Tertiary continental deposits pass into brackish water and near-shore marine deposits. According to Lowman (1949, p. 1941), rapid transgressions and slow regressions produced cyclical effects in the sediments with most of the sediments deposited during the regressive phases of the cycles. Farther down-dip or seaward the sediments change to a succession of offshore marine clays.

In general, the Gulf coastal area may be divided into intergrading depositional areas as follows: Rio Grande Embayment, East Texas Basin, Mississippi Embayment, the Gulf coastal region of Alabama, Georgia, and North Florida, and South Florida. The amount of rainfall on the land area surrounding the ancient Gulf may have been the chief factor in determining the contemporaneous deposition of many sedimentary deposits ranging from anhydrite and salt to shales and limestones. Rolshausen (1947, p. 5) suggested that during pre-Eagle Ford Cretaceous time, west of the Appalachian Mountains, rivers entering the Gulf from the north and northeast supplied the major load of sediments. East of the mountains the rivers entered the Gulf from the northwest and west. After Eagle Ford time, rivers entering the Gulf from the west, and probably draining the western part of the present Mississippi basin, were the chief source of sediments. The Rio Grande may have been the major source of sediments from the late Cretaceous through early Miocene time with the Mississippi River contributing little sediment during that time.

PLACE OF DEPOSITION

The sediments brought to the Gulf of Mexico are probably not carried far from shore. Parr (1935, p. 62) showed that at a point only 70 miles out in front of the mouth of the Mississippi River the water has "transparency practically equal to the clearest ocean water known." It is a generally accepted fact that water discharged from the Mississippi River is carried almost entirely to the west and that it stays relatively close to the shore. Clarke (1938, p. 91) found that measurements of transparency supported this conclusion. Geyer (1950b, p. 100) noted that the salinity of the offshore coastal waters of Louisiana west of the delta was largely controlled by the discharge of fresh water from the Mississippi River and the westward moving littoral current. The observations of the writer between 1948 and 1951 confirm the westward movement of the fresh water entering the Gulf from the Mississippi River.

Cogen (1940, p. 2101) examined samples of sediments taken from the bottom of the Gulf near the mouth of the Rio Grande and concluded that the present bottom sediments of this region were carried into the Gulf by the Rio Grande.

Bullard (1942, pp. 1021–1043) showed that each of the principal rivers carries a distinct suite of heavy minerals. The Rio Grande sand shows its primary source by the predominance of basaltic hornblende and pyroxene and only 30 percent of the stable minerals such as garnet, rutile, zircon, tourmaline, and staurolite in the heavy mineral residue. The Nueces, San Antonio, Brazos, Trinity, and Sabine Rivers, draining areas of sedimentary rocks, have little hornblende and pyroxene and a high content of stable minerals. Since the Colorado River derives its load from both primary and secondary rocks, its suite of heavy minerals is over half green hornblende. Northward from the Rio Grande the beach of Padre Island contains the Rio Grande suite of heavy minerals, but the influence of the other rivers is clearly shown by an increased ratio of more stable minerals in the samples farther north in Texas.

The sediments of the Coastal Plain do not end at the shore but extend out under the sea, and "if the basement surface on which they rest continues to slope uniformly, the mass of sediments must increase in thickness at least as far as the edge of the continental shelf, beyond which they should thin out rapidly as they merge into the oozes of the ocean depths" (Stephenson 1926, p. 463).

Land derived sediments are not being moved in a "continuous sheet of detritus all the way from the beach to the continental slope" (Daly 1942, p. 100). If this were true, much of the continental shelf would be some fathoms shallower than at present. With continuing deposition the sea would become more shallow, and wave and current action would push the sediments nearer the edge of the shelf. When the sediments reached the edge of the continental shelf and a profile of equilibrium was attained, the shelf sur-

face would have been raised several fathoms. Therefore, it appears that a profile of equilibrium does not exist on the outer part of broad Gulf of Mexico continental shelves.

Sediments carried to the Gulf of Mexico largely remain in that body of water rather than being carried into the Atlantic. The Gulf of Mexico is of no importance to the deep-water circulation of the Atlantic Ocean (Kuenen 1950, p. 44). The unnamed current that becomes the Florida current is the major current of the Gulf, and "it is essentially a direct continuation of the current through the Yucatan Channel" (Sverdrup, Johnson, and Fleming, 1942, p. 642). The waters of the Gulf mainly form independent eddies and are only to a small extent drawn into the Straits of Florida. These eddies appear to be semipermanent features with their locations determined by the contours of the coast and the configuration of the bottom (idem., p. 641).[3]

EARLY STUDIES OF SUBMARINE DEPOSITS

The Coast Survey instituted a series of investigations on physical problems of the deep sea in 1846, with emphasis on the Gulf Stream. In 1850, L. Agassiz made an extended biological survey of the Florida reefs, and in 1867, Pourtalès and Mitchell began a more systematic deep-sea exploration. Dredging between Florida and Cuba in 1868 reached depths of 850 fathoms, and the bottom samples obtained showed a closer relationship to the cretaceous fauna rather than to organisms of the adjacent shores.

Commander Howell, U. S. N., began a systematic exploration of the Gulf of Mexico in 1872, starting in the shallow waters along the west coast of Florida, and the work was continued by Lieutenant Commander Sigsbee in 1875–78, using the United States Coast Survey steamer *Blake*. The specimens of bottom deposits were sent to John Murray of the *Challenger* for examination, and he published the results in 1885 (Murray, pp. 51–61). Excerpts from his original description are as follows:

> In all the deeper deposits in the Gulf of Mexico and Strait of Florida, the crystalline mineral particles are very small, rarely exceeding one-tenth of a millimeter in diameter. They consist principally of small rounded grains of quartz, with fragments of felspars, mica, hornblende, augite, magnetite, and rarely tourmaline. In a few places there were fragments of pumice, and glauconitic particles were occasionally noticed. The mineral particles and fine clayey matter appear to be almost wholly derived from North American rivers.
>
> The carbonate of lime in the deposits of these regions is mostly made up of the shells of pelagic Foraminifera and Mollusks. In depths greater than 2,000 fathoms the Pteropod and Heteropod shells appear to be nearly, if not quite, absent—the carbonate of lime then consisting of the shells of pelagic Foraminifera; in less depths the Pteropod and Heteropod shells are present, and in depths varying from 200 to 500 fathoms they make up the bulk of the deposits in many places. In several of the deposits, where the percentage of carbonate of lime is very high, the whole has a very chalk-like appearance; it appears, indeed, as if it were in the process of transformation to true chalk.
>
> The siliceous organisms consist of Radiolarians and Sponge spicules, with a few Diatoms, but these seldom make up more than three or four percent of the whole deposit.

A study of the United States Coast and Geodetic Survey maps of the continental shelf adjacent to Louisiana shows many different materials forming the Gulf bottom such as sands, muds, clays, shells, and local reefs. These represent the surface of the Gulf floor, and little is known about the material even immediately below the surface. Some borings have been made in the erection of the platforms required for petroleum exploration, but these platforms are all located approximately within the first 30 miles off shore. The wells drilled from these offshore structures have yielded no known information of the surface formations. Likewise, crews making geophysical surveys in the Gulf are not interested in the surface or near-surface formations (Willey 1948, p. 3).

Trowbridge (1927, p. 148) stated that the United States Coast and Geodetic Survey obtained 600 bottom samples in 1921 and that their map of 1926 included the results of this work.

RECENT STUDIES OF SUBMARINE DEPOSITS

According to Trask, Phleger, and Stetson (1947, p. 460) sediments in the Gulf of Mexico have changed in relatively recent time. During the 1947 expedition of the *Atlantis*, more than 600 cores were taken along 19 lines perpendicular to the Texas and Louisiana coast, crossing both the continental platform and the continental slope and continuing into the depths of the Gulf. The complete results of this expedition have not been published to date, but some data were discussed by Phleger (1950). It was found

[3] For a detailed discussion of circulation of water in the Gulf of Mexico see article by D. F. Leipper, Physical Oceanography of the Gulf of Mexico, in this book, pp. 119–137.

that sediments off shore were remarkably uniform. Out to a distance of some 40 miles from shore a combination of fine sand and coarse silt with an average diameter of 100 microns was found; this material was extremely well sorted. On the outer shelf the sediments were much finer, the average diameter being about 1 micron, and they were poorly sorted. In water over 11,000 feet deep in the central part of the Gulf foraminiferal ooze at the surface was underlain, beginning at 2 feet depth, by alternating clay, silt, and sand, the silt and sand being extremely well sorted.

A core taken in the Mexican Basin in 1947 is of unusual interest. Trask, Phleger, and Stetson (1947, p. 461) reported that:

> The upper foraminiferal zone, 50 cm. in thickness, is characterized by a subtropical planktonic fauna . . . Between depths of 50 and 68 cm. in a zone of red clay or red mud, the fauna is transitional between cold and warm water faunas. Between depths of 74 and 78.5 cm., at the top of the zone of banded clay and silt, the fauna is definitely sub-Arctic . . . Between 78.5 cm. and 125 cm., the fauna is cold-water in type but is warmer than that between 74 and 78.5 cm.; and from 125 to 128 cm., at the bottom of the core, the fauna is definitely sub-Arctic.

Trask (1948, p. 683) mentioned that ice-age deposits showing crossbedding or ripple marks were found in the coarse clastics of two cores taken in the central Gulf of Mexico. In other cores "well-sorted sand zones, one and three feet, respectively, were encountered at depths of more than three feet beneath the surface of the sediments. Such deposits, if hardened into rock and formed in a geosyncline, would be taken as compatible with the idea of shallow-water deposition. Yet they were encountered in 11,000 feet of water."

The Fish and Wildlife Service of the United States Department of the Interior, cooperating with the Agricultural and Mechanical College of Texas, is making a systematic survey of the Gulf of Mexico. Much of the physical oceanography is being done by the Texas A. and M. Department of Oceanography, and the Department of Geology is cooperating in the study of Gulf problems of marine geology. Samples of sediments obtained early in 1952 are now being studied.

SEDIMENTARY PROVINCES

The major sedimentary provinces of the Gulf are shown on the map in figure 16. The basic data for this map were collected from many sources, including the publications of Agassiz, Carsey, Gunter, Kindle, Lowman, Murray, Phleger, Price, Shepard, Stetson, Trask, and Weaver, and by personal communications from individuals principally W. A. Price, Department of Oceanography, Agricultural and Mechanical College of Texas. Unfortunately, the data resulting from some 600 cores taken from the *Atlantis* in 1946 are not yet available. Also, the systematic exploration of the Gulf now in progress will provide many bottom samples from the whole Gulf area, and these data will make possible more detailed sediment maps in the future.

The recent sediments are divided into lithological units which form somewhat indefinite zones parallel to the coast and extending outward on the continental shelf. In general, sands and shales predominate from Florida west and south to Cabo Rojo, Mexico, while limestone forms a wide platform west and north of the Yucatán Peninsula and west of Florida.

EASTERN GULF

Modern calcareous sediments were thought by Agassiz (1888, p. 286) to cover the continental shelf on the west side of Florida. The charts of this area show "sand and shells" and are therefore deceiving. Samples from this region that were examined by Shepard (1932, p. 1021) "were lacking in quartz-sand and the use of sand as a textural term seemed questionable." Little sediment goes to the Gulf in streams from the Florida Peninsula, and the shore deposits consist largely of calcium carbonate secreted by organisms. Even the Apalachicola River does not discharge an appreciable amount of clay and silt. However, some quartz sand is found relatively near shore from Mississippi eastward across Alabama and the panhandle and near shore along the northern part of the west coast of Florida. Also, recently, numerous sand bars have been found on the northern part of the continental shelf west of the Florida Peninsula.

The area off shore from Alabama and the panhandle of Florida has detrital sediments which show the influence of the southern Appalachians. These sediments contain an abundance of ilmenite, staurolite, kyanite, zircon, tourmaline, and sillimanite, and only minor amounts of magnetite,

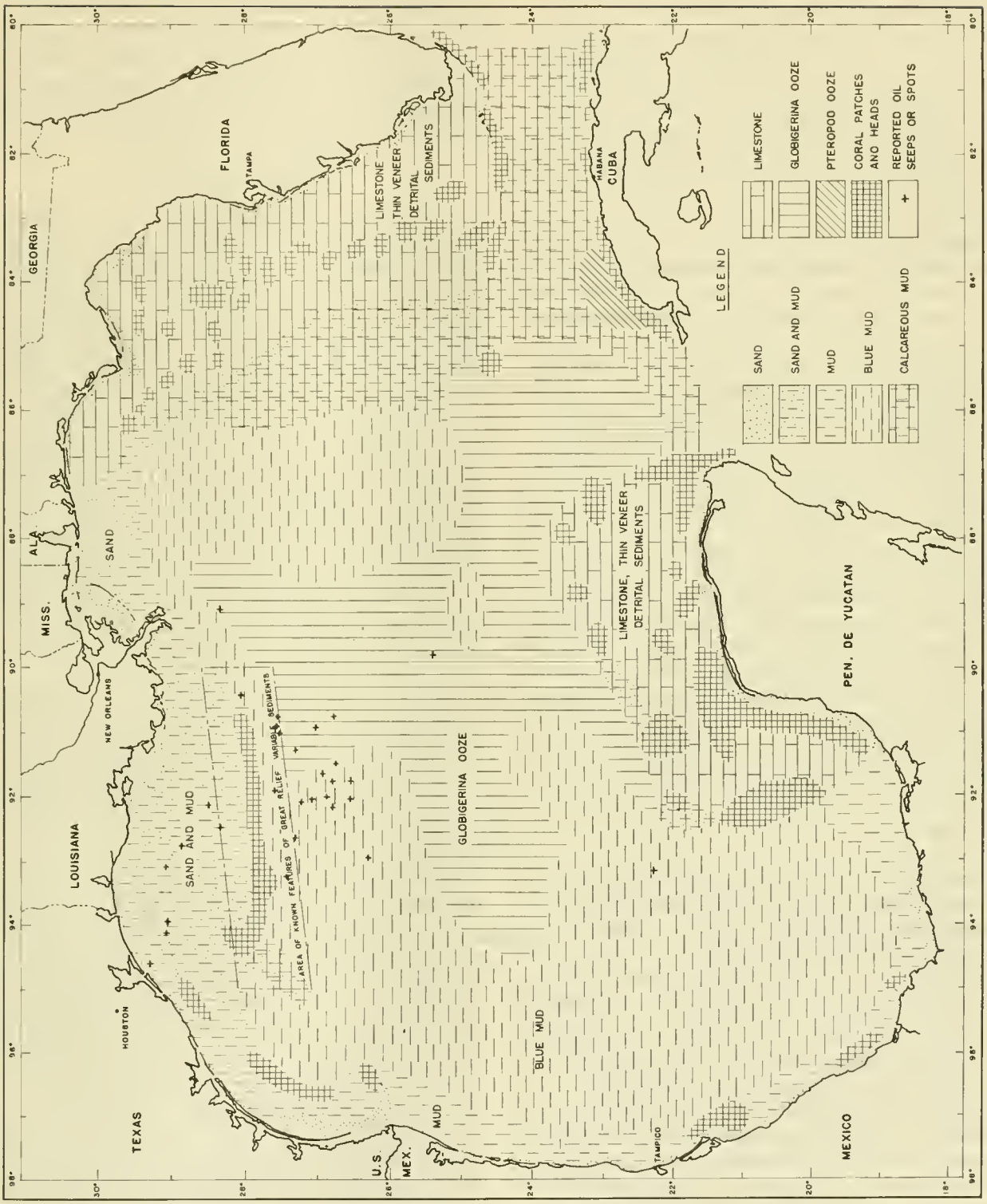

FIGURE 16.—Sedimentary provinces of the Gulf of Mexico. Data compiled from many sources.

amphiboles, pyroxenes, leucoxene, and hematite (Goldstein 1942, p. 81).

Most of the continental shelf west of the peninsula of Florida is hard rock, chiefly limestone, but a thin veneer of detrital sediment is present in local areas and fills some of the shelf depressions. Stetson (1951, p. 1993) obtained two specimens of hard limestone and a specimen of soft, chalky limestone from this shelf by using a steel rock dredge after core tubes were damaged by the hard rock.

The Florida Keys include a 200-mile chain of islands curving southwestward along the edge of the Florida Straits from Biscayne Key to Key West and the Dry Tortugas. The northeastern keys are old coral reefs, but the ones to the southwest are remnants of a former island. Vaughan (1910, p. 119) stated that silica, as sand, is abundant in Biscayne Bay but decreases to the southwest as calcium carbonate becomes more abundant near the living coral reefs. The calcium carbonate occurs "as a flocculent sediment or ooze over practically the entire region from the lower portion of Biscayne Bay to the gulf end of Florida Bay." However, Trask (1932, pp. 166–172) found that the basins in Florida Bay have coarser sediments than the compact marl rims. The basin sediments are "shell breccia embedded in a matrix of marl."

The recent work of Lowman (1951, pp. 234–235) provided the basis of division of the limestone banks west of Florida. He found that the white sands of the Pensacola beaches extended seaward to the depth of 20 fathoms and that the sands were free of mud and were highly fossiliferous, with Mollusca and Foraminifera being the most common forms.

A second zone, extending out to 40 fathoms, was found to contain many algae, forams, pelecypods, brachiopods, bryozoans, and cup corals. The Foraminifera showed a definite faunal break at about 75 fathoms which Lowman (idem., p. 235) suggested may be the result of changes in turbidity and light penetration in the clear water. In the more turbid waters west of the Mississippi Delta a faunal break was noted at 45 to 50 fathoms.

Bush (1951, pp. 102, 106) reported on a rock specimen obtained by dredging in the Straits of Florida, south of the American Shoals, at a depth of 375 fathoms. This rock, apparently broken from the ocean floor, was very fossiliferous and was correlated with the Chipola formation (lower Miocene) of northern Florida. This suggests "the dip and continuance of the lower Miocene strata from the Florida Peninsula under the Straits of Florida toward Cuba" (idem., p. 106).

Between the Florida Straits and Cuba and also west of the continental shelf the bottom sediments are calcareous muds, and westward they grade into blue mud and Globigerina ooze.

MISSISSIPPI DELTA

Most of the coarse sediment of the Mississippi River is deposited near its mouth, but Trowbridge (1930, p. 892) noted that outside the Southwest Pass of the river, coarser sediment occurred on knolls in 30 fathoms of water. This coarser sediment apparently was not derived from the present Mississippi River under present conditions. The concentration of coarse sediments may have resulted from the removal of the finer sediments by winnowing due to stronger currents over the knolls.

Shaw (1916, p. 107) stated that fine sand, silt, and clay were accumulating on the Gulf of Mexico floor immediately beyond the mouth of the Mississippi River very near where they were dropped by the river. He contrasted this with conditions on the west Gulf coast where the sediments brought to the Gulf by streams were being reworked by waves and currents yet not carried far from the mouths of the streams.

Mud and sand are recorded on many maps on either side and adjacent to the Mississippi River, but sampling by the writer shows silt and "mud" to be greatly in excess of sand. Westward from the delta there is a clay-silt zone with some sand and shells. Dark gray to black "mud" is present in most of the lagoons.

Kellogg (1905, p. 34) and many others, including the writer, have observed the hard crust that develops during the winter. This crust is only an inch or two thick and is underlain by soft silt and "mud." The clay and finest particles have probably been removed by winnowing during the winter when the Mississippi River is in a low stage and therefore carrying a minimum sediment load.

The very high ratios of organic matter to chlorophyll which occur near the mouth of the Mississippi River "indicate large quantities of organic detritus. The ratios fall so rapidly as one proceeds out in the Gulf that it seems likely that practically all the organic detritus of fresh water origin is removed from the surface water

before it gets more than ten or fifteen miles from the mouth of the river" (Riley 1937, p. 91).

It is noted in figure 16 that the blue mud province extends northward to near the mouths of the Mississippi River. Since the front of the delta overlaps the continental shelf nearly to its outer edge, the sediments of the deeper Gulf approach the tip of the delta. Likewise, the Globigerina zone lies close to the land at the delta.

LOUISIANA SHELF

The numerous submerged hills rising above the sea floor near the outer edge of the continental shelf materially influence the local sediments. Trask, Phleger, and Stetson (1947, p. 461) noted that the slopes of these hills are covered with "silty, calcareous sand, and the tops by round *Lithothamnium* balls and little or no sandy material . . . while the adjacent flat continental shelf is underlain by sandy silt." The *Lithothamnium* balls, diameters up to 10 cm., must have been moved by the water since they seemed to be alive on all sides. Corals, similar to those common in the West Indies, were dredged with the *Lithothamnium* balls. These areas are included in figure 16 in the patches of coral lying along 28° N. lat. between 91° and 95° W. long.

The dominant sediment on the continental shelf along the Louisiana coast west of the Mississippi Delta is mud and sand. Locally, near shore, sand predominates to form a sand beach and shore zone. The common, heavy minerals of these sediments are amphiboles, epidote, dolomite, pyroxene, ilmenite, and biotite.

Near the outer edge of the shelf and particularly on the continental slope there are many topographic features of considerable relief. Carsey (1950, pp. 377–379) noted 164 such topographic features along the Louisiana-Texas slope and made a study of their density distribution according to their degree of relief. This study showed that two-thirds of these features have a relief of less than 300 feet, while some rise 600 feet above the floor of the Gulf.

The sediments on the tops and flanks of topographic features, having a relief in hundreds of feet, may be greatly different from those on the ocean floor only a short horizontal distance away. Corals have been dredged from the tops of a few of these knobs or domes, but little is known concerning the deposits on the flanks. The finer sediments may have been washed from the tops of these knobs to settle on the Gulf floor around the base. More detailed sounding and dredging in this area are needed to adequately study the sedimentology of the area.

Over a 50-year period numerous "oil spots" or "seeps" have been reported as having been observed in the northwest Gulf of Mexico. The locations of these seeps are noted on the map (fig. 16), and it is seen that they are concentrated between 91°–93° W. and 26°30′–27°30′ N. Since several of these "oil spots" were said to be several scores of miles long, their origin, although unknown, is of interest.

WESTERN GULF

The rivers of Texas are not heavily laden with sediment, except during flood stages, and for this reason it can be assumed that the Recent alluvial deposits found on the continental shelf will not be of great thickness. Also, these streams have little velocity as they cross the wide coastal plain, and only fine-grained mechanical sediments are carried to the Gulf. This has been shown by Storm (1945, p. 1313) in a series of samples collected in the Gulf out from Corpus Christi, Texas. Beyond the near-shore fine material sands with 0.21 millimeter average diameter occurred in a narrow belt about 12 miles from shore. Twenty miles from shore the grain size had decreased to an average of 0.03 millimeter, while 30 miles from shore it had increased to an average of 0.18 millimeter. From 30 to 40 miles off shore the grain size remained about the same, but beyond 40 miles it decreased again. These variations seem to be closely associated with the currents.

In 1948 Mattison (p. 77–78) found a string of coral heads off the Brazos River mouth about 8 miles off shore. They occur in 6 to 8 fathoms of water and have a relief of 2 to 3 fathoms. They have been seen by fishermen who describe them as having the appearance of sunken icebergs but having sea fans and other marine growth forming solid coral or white limestone in an area of black mud. Coral heads occur approximately along the 40-fathom line in front of Corpus Christi, Texas, and Smith (1948, p. 82) noted that six of these heads were reached within a foot or two of 31 fathoms of water.

Along most of the east coast of Mexico from Texas to the Gulf of Campeche the charts show

"sand" near shore and "mud" off shore, showing an outward gradation of sediments.

Agassiz (1878, p. 1) found the fauna of the Yucatán Bank to be identical with that of the Florida Bank, being characterized by the same species of echinoderms, mollusks, crustaceans, corals, and fishes.

From Tampico southward beyond Veracruz volcanic rocks are found near shore, and possibly igneous rocks will be found in the adjacent Gulf waters. Therefore, the sediments in this area should be somewhat different from those off southern coastal Texas and from those associated with the limestone of the Campeche Banks to the east. The coastal plain is exceedingly narrow locally, and the beach sands give way to near-shore patches of coral. In many places mud extends out on the shelf beyond the coral.

YUCATÁN PENINSULA

The beach sands along the west and north shores of the Yucatán Peninsula do not spread far from shore except locally where sand and mud are found out to the edge of the shelf. To the southwest of the peninsula the sand becomes mixed with near-shore coral patches.

Numerous local patches of coral occur over the Campeche Banks, and in other places the bottom is very similar to the Florida Bank. The hard limestone is locally covered with a thin veneer of detrital sediments. The Globigerina ooze province joins the Campeche Banks apparently with the blue mud absent between these calcareous sediments.

CUBA

Corals are common at the outer edge of the narrow shelf off the northern coast of Cuba. Beyond these corals the Florida Straits contain calcareous mud with the exception of a local area to the northwest of Cuba where pteropod ooze has been found.

A bottom sample taken in 20 fathoms of water at 24°25′ N. lat. and 82°26′ W. long. was subjected to a chemical and spectrographic analysis. Also, use was made of electrolytic separation in a mercury cathode cell to concentrate the trace elements. No unusual trace elements were found, and the common elements were in approximately the same abundance as has been determined by others who analyzed the skeletal material of organisms which contribute to sediment formation.

MEXICAN BASIN

The upper surface of the floor in the deepest part of the Gulf consists of foraminiferal ooze. The few available cores show the underlying sediment to be clay, silt, and sand, which is cross-bedded and ripple-marked in some cores. The origin of this detrital material is unknown as is also the origin of the basin forming the Gulf. Turbidity currents may have brought much sediment to the central Gulf. Such an origin is further suggested by the presence of continental-shelf Foraminifera in the Mexican Basin sediments.

Agassiz (1888, pp. 280–282) quoted Murray who observed that the globigerine and pteropod ooze found in the central Gulf of Mexico differed materially from that found in the oceanic basins. Diatoms, radiolarians, and sponge spicules comprise the siliceous organisms but represent only a small percentage of the bottom deposits. Fish otoliths were found at depths from 392 to 1,568 fathoms. The globigerine ooze was found to extend northward to the Mississippi River slope where it was replaced by dark, rich muds containing "a number of interesting forms of annelids, mollusks, ophiurous and sea-urchins, characteristic of the continental Gulf slope, and typical of mud deposits" (idem., p. 282).

CONCLUSIONS

The Gulf of Mexico, with a surface area of 615,000 square miles, offers many rewards for research in geology, biology, and oceanography. Continued drilling at the extreme margins of the Gulf may produce new local data as greater depths are reached by the drill, but much of the search must be made far from shore. To date most of the geophysical prospecting has been in the very shoal areas where present methods of development may apply. The use of geophysics to study the tectonics of the Gulf largely lies in the future. Therefore, it seems that present aid in solving the many problems of the Gulf of Mexico must come from the oceanographer who can give other scientists new data from soundings, bottom samples, and the physical characteristics of the water.

While the time and manner of the origin of the Gulf basin are still undetermined, present evidence favors the existence of a shallow Gulf, the "plate" of Suess and Schuchert. Assuming that Llanoria

extended into the Gulf, its submergence may have been completed by late Jurassic time, thus providing for the invasion by the Cretaceous seas. Post-Cretaceous downwarping tilted the Cretaceous deposits Gulfward, but, in general, the Gulf remained a shallow sea during most of the early Tertiary. During late Tertiary the basin of the Gulf further subsided, possibly both by downwarping and faulting along the basin margins. The escarpment along the west edge of the Florida shelf (Jordan 1951, pp. 1978–1993) undoubtedly has its origin in faulting, and similar conditions seem to exist at the outer edge of the Campeche Banks. Other areas along the continental slope suggest fault scarps. The basin of the Gulf may well have been deeper than the present 12,425 feet, with post-mid-Tertiary sediments filling the basin to its present depth.

There is no reason to believe that the irregularities of the continental slope are confined to the local areas which have had detailed study, and further hydrographic work should produce data of great scientific value.

Interest in the Gulf has been greatly accelerated in the past decade, and there is much evidence that this interest will continue, which should result in the eventual solution of many of the present riddles of the Gulf of Mexico.

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CHAPTER III

MARINE METEOROLOGY OF THE GULF OF MEXICO

MARINE METEOROLOGY OF THE GULF OF MEXICO, A BRIEF REVIEW[1]

By DALE F. LEIPPER, *Department of Oceanography, Agricultural and Mechanical College of Texas*

The best general summary of the weather over the Gulf of Mexico in nontechnical language is probably that prepared by the United States Weather Bureau for the United States Coast Pilot (1949).[2] There are a number of articles on the general circulation of the atmosphere and on meteorological processes without specific reference to the Gulf of Mexico which, nevertheless, pertain to this region as well as to all similar regions. It will not be attempted to review such articles in the present summary. Two references of this type are Holmboe, Forsythe, and Gustin (1948), and Byers (1944). In addition, there are some publications such as Riehl (1947) which deal with the general weather in the low latitudes and are helpful in understanding the Gulf of Mexico weather more completely.

EXTRATROPICAL CYCLONES

Saucier (1949) has analyzed the frequency and behavior of extratropical cyclones originating on or near the northwestern coast of the Gulf of Mexico over a 40-year period. These cyclones have marked effect upon the weather of the Gulf as well as upon that of much of the eastern United States. They occur on the average about 10 times per year with a maximum number of 19 occurring in 1899 and a minimum of 2 in 1916. The high frequency of these storms appears to result from the influence on the general circulation of the warm moist surface provided by the Gulf of Mexico, the cold continental air to the north, and the mountains to the west. It was found that the cyclones seldom occurred immediately after a deep cold air mass penetrated the entire Gulf of Mexico but were most common when it remained north of the Gulf coast. The storms may begin as early as October. The maximum number occurs in January. Very few occur later in the spring than April. The regions of formation, directions of motion, and the characteristics of the intensification of the 388 cyclones studied are discussed.

THE GENERAL AIR CIRCULATION AND SOME OF ITS CONSEQUENCES

The Bermuda atmospheric high pressure cell dominates the circulation over the Gulf, particularly during the spring and summer months. In the late summer there is a general northward shift of the circulation and, as shown in figure 17, the Gulf comes under the more direct influence of the equatorial low pressure belt. The constancy of the Bermuda high tends to maintain steady circulation and to govern the climate during the summer. Summer conditions are illustrated in figure 18. No isotherms appear for average water temperature (sea surface temperature) since the waters are nearly uniform at about 84° F. as illustrated in the chapter on physical oceanography.[3] The air temperatures on the average are also quite uniform and high. The southerly position of the Bermuda cell brings about the southeast–northwest orientation of isobars across the Gulf and leads to a predominance of southeasterly winds, as shown by wind arrows. The winds tend to become more southerly in the northern part of the Gulf. In this region there are practically no northerly winds in summer and only a relatively few from the east or the west. In the more southern parts of the area the predominance of the easterly and southeasterly flow is even more marked.

With a typical summer circulation in the Gulf and the uniform average sea surface temperature, there would be expected only a minimum number of local weather features over the water which are the type caused within the Gulf by air flow toward successively warmer or cooler water surfaces. However, on a larger scale the relatively

[1] Contribution from the Department of Oceanography of the Agricultural and Mechanical College of Texas, Oceanographic Series No. 20. Based in part upon work done under the sponsorship of the Office of Naval Research and the Air Force Cambridge Research Center.

[2] References are listed at the end of the chapter.

[3] See Physical Oceanography of the Gulf of Mexico, p. 119.

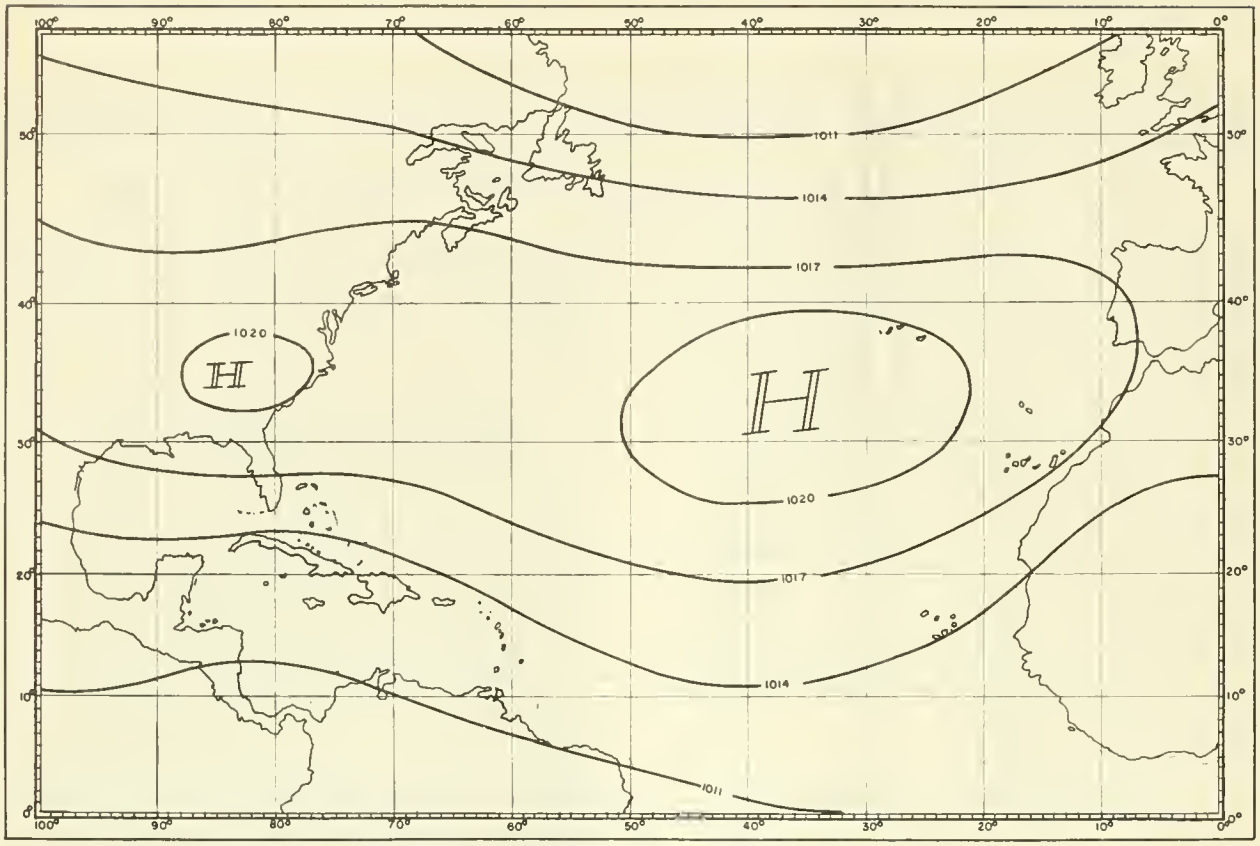

FIGURE 17.—Normal sea level pressure, October.

high temperature of the Gulf of Mexico waters compared to those of other water surfaces in the same latitudes brings about such a great warming and increase in the moisture content of the overlying air masses that weather patterns of the area are markedly affected. (The mean annual surface temperature of the Gulf is 78° F., while that of a comparable region at the same latitude in the western Atlantic is 76°, in the eastern Atlantic 73°, and in the eastern Pacific 68°).

Typical features of the winter circulation are shown in figure 19. Here the winds are more from the easterly directions with fewer southerlies but more northerlies. There are very few winds from the west or the southwest. The sea surface temperature pattern shows a variation from more than 75° F. in the southeastern portion to less than 65° in the northwest. Southeasterly winds bring warm, moist air from lower latitudes and carry it from warmer toward colder water in the Gulf. When this flow is slow and sustained, the cooling by the ocean surface leads to condensation and fog and stratus formation in the northern Gulf.

A discussion of the upper air circulation for the Gulf and Caribbean area is given by Erna and Rudolf Penndorf (1944).

AVERAGE CONDITIONS

Average sea-level atmospheric pressures in the Gulf vary from 30.00 to 30.15 inches of mercury. There are wide deviations from these averages in individual synoptic situations. Worthy of note is the diurnal pressure variation with a lesser early morning minimum followed by a greater late morning maximum and evening minimum and a lesser nocturnal maximum.

The Atlas of Climatic Charts of the Oceans, published by the United States Weather Bureau, and the Pilot Chart of Central American Waters, published by the Hydrographic Office of the United States Navy, issued monthly, give further information about the winds, pressures, tempera-

tures, and other weather features of the Gulf of Mexico. The average wind velocity varies from 6 to 8 knots in the summer, with the stronger winds in the southeast portion, to 10 to 12 knots with considerable variability in the winter, the higher averages being in the northeastern portions.

Fog is most frequent in midwinter when as high as 10 percent of all observations record light or dense fog in the north central part of the Gulf. In this season fogs occur less than 1 percent of the time in the southeastern portion.

For the year-round the average cloud-cover over the Gulf is $\frac{1}{10}$ to $\frac{6}{10}$ of the sky obscured. In winter and spring the areas most obscured are in the north and northwest, while in the summer and fall the southern and southwest portions have the highest average cloud cover. The most commonly reported low type clouds are cumulus

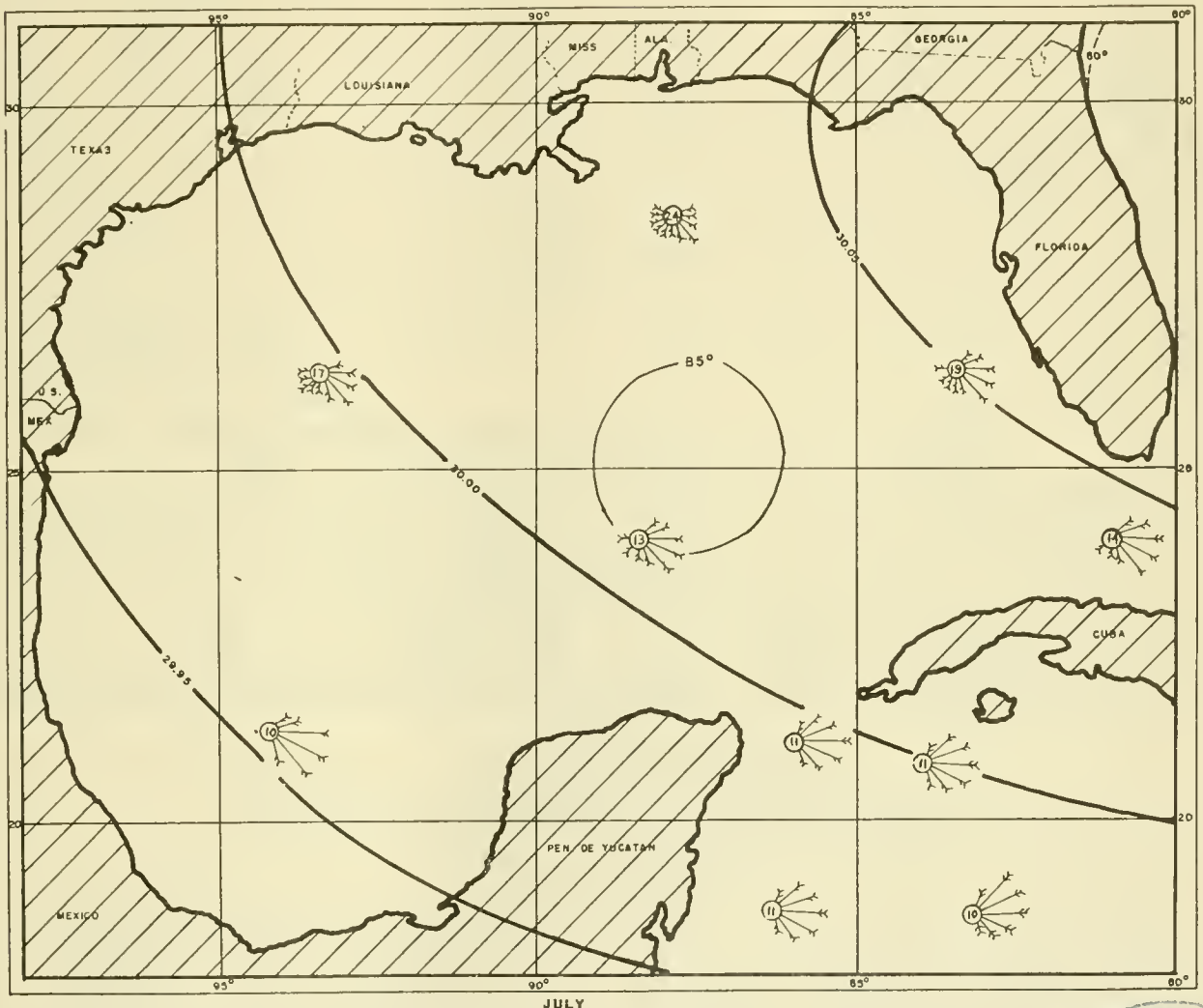

FIGURE 18.—Average sea level pressure (inches) and average air temperature (°F.), July.

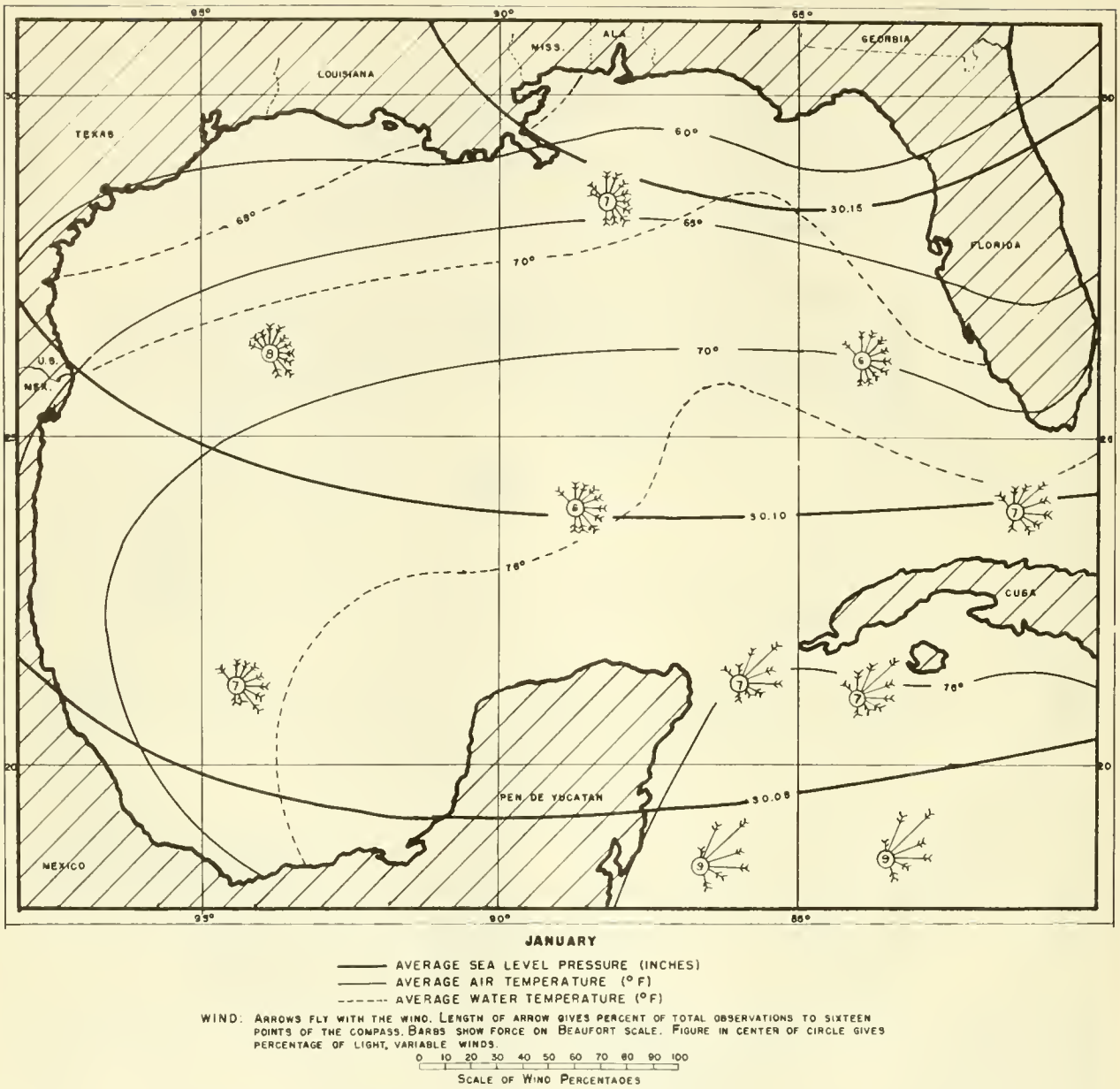

FIGURE 19.—Average sea level pressure (inches), average air temperature (°F.), and average water temperature (°F.) January.

which have the greatest frequency—greater than 30 percent of all observations—in the summer and fall in a band extending from the Yucatán Channel northwestward across the Gulf. Altostratus and altocumulus are common the year-round, their average frequency being from 10 to 20 percent throughout the Gulf. In the summer and fall cumulonimbi are observed about 10 percent of the time in the western and northwestern regions.

The period of lowest occurrence of rainfall over the open water is in the spring when less than 5 percent of the observations show rain according to the Atlas of Climatic Charts of the Oceans. The remainder of the year the frequency is 5 to 10 percent over most of the Gulf except for an area around the Yucatán Peninsula where frequencies drop below 5 percent in the winter and summer. A study by Kloster reported in the

Coast Pilot shows rain in from 13 to 21 percent of the hourly observations available for the entire year between 22½° to 27½° N. latitude and 80° to 90° W. longitude. Rainfall was most frequently reported in the mid afternoon—19 percent versus 15 to 17 percent at other times of the day.

The average depression of the wet bulb is 3° F. for the fall quarter—September, October, and November. During the remainder of the year it is 2° for the western Gulf and 3° for the eastern.

In the summertime the air and the sea surface differ in temperature by less than 1°, the sea temperature being higher according to the Atlas of Climatic Charts of the Oceans. In the fall and winter differences increase, with the sea temperature being as much as 5° higher than the air temperature in the area just west of the Florida Peninsula. This leads to heating from below on the average and explains the high frequency of cumulus-type clouds over the Gulf. Monthly average sea surface and air temperatures are tabulated in the chapter on physical oceanography (p. 119).

WEATHER OBSERVING STATIONS

It is the purpose of this summary to discuss weather over the water in the Gulf. Since the observations here are sparse, some of the conclusions are drawn from observations made on the surrounding land areas. The weather observing stations in these areas are shown in figure 20. Those on the coast are listed in table 1. A particularly interesting feature of the Gulf is that

TABLE 1.—*Weather observing stations along the coast of the Gulf of Mexico*

Station number	Location	Station number	Location
201	Key West, Fla. (NAS).	642	Nautla, Veracruz.
211	Tampa, Fla. (International Airport).	692	Veracruz, Veracruz.
214	Tallahassee, Fla. (Dale Mabry Field).	741	Coatzacoalcos, Veracruz.
220	Apalachicola, Fla.	743	Villa Hermosa, Tabasco.
222	Pensacola, Fla.	746	Ciudad Obregon, Tabasco.
223	Mobile, Ala.	749	Ciudad del Carmen, Campeche.
231	New Orleans, La.	695	Campeche, Campeche.
232	Burrwood, La.	643	Merida, Yucatán.
240	Lake Charles, La.	648	Cozumel, Quintana Roo.
241	Port Arthur, Tex.	751	Chetumal, Quintana Roo.
242	Galveston, Tex.	501	Swan Island, West Indies.
243	Houston, Tex.	395	Vernam Field, Jamaica.
255	Victoria, Tex.	397	Kingston, Jamaica.
251	Corpus Christi, Tex.	325	Havana, Havana (Casa Blanca).
250	Brownsville, Tex.	244	Cienfuegos, Santa Clara.
491	Ciudad Victoria, Tamaulipas.	355	Camaguey, Camaguey.
349	Ciudad Camargo, Tamaulipas.	367	Guantanamo, Oriente.
639	Tuxpan, Veracruz.	265	Antilla, Oriente.

although it covers some 700,000 square miles, it is more than 90 percent surrounded by land. The rather complete coverage of weather information around its perimeter makes it an unusual natural laboratory in which to study changes in the character of air masses as they pass across the large body of water.

TYPICAL UPPER AIR SOUNDINGS

A comparison of the upper air soundings from Swan Island, south of the Gulf, with those of New Orleans and Brownsville, on the north and northwestern coasts, illustrates the modifying effects of the water surface. Monthly average radiosonde observations for a summer month and a winter month at each of these stations are shown in figure 21. It will be noted that the annual change in structure at Swan Island, which is almost completely controlled by oceanic factors, is very small, the most noticeable change being the higher relative humidities in the summer. At Brownsville and New Orleans the sea surface is cooler in winter, but, also, the continental influence tends to make winter temperatures definitely lower than those in summer.

A rather complete discussion of the tropical Gulf air mass is given by Willett (1943). He states that the uniformity of the water temperature in the source regions of tropical maritime air masses has proved to be of more importance in fixing the properties of the masses at all levels than has the previous life history of the individual air masses. Evidence is given demonstrating that the structure of the lower stratum of the air mass results from the turbulent mixing of saturated air. The air masses are characterized by marked potential instability, implying that all convective or mechanical turbulence up to at least 5 kilometers elevation must effect an upward transport of latent heat. The high relative humidities indicate that active convection extending above this level can be initiated by very little vertical displacement. Summer thunderstorms are more likely along the eastern part of the northern Gulf coast than along the western. There are higher relative humidities in the eastern area.

Using a series of atmospheric temperature and moisture soundings to 45 feet elevation made at 4-hour intervals in March 1949 from an oil platform in the northwestern Gulf, Gerhardt

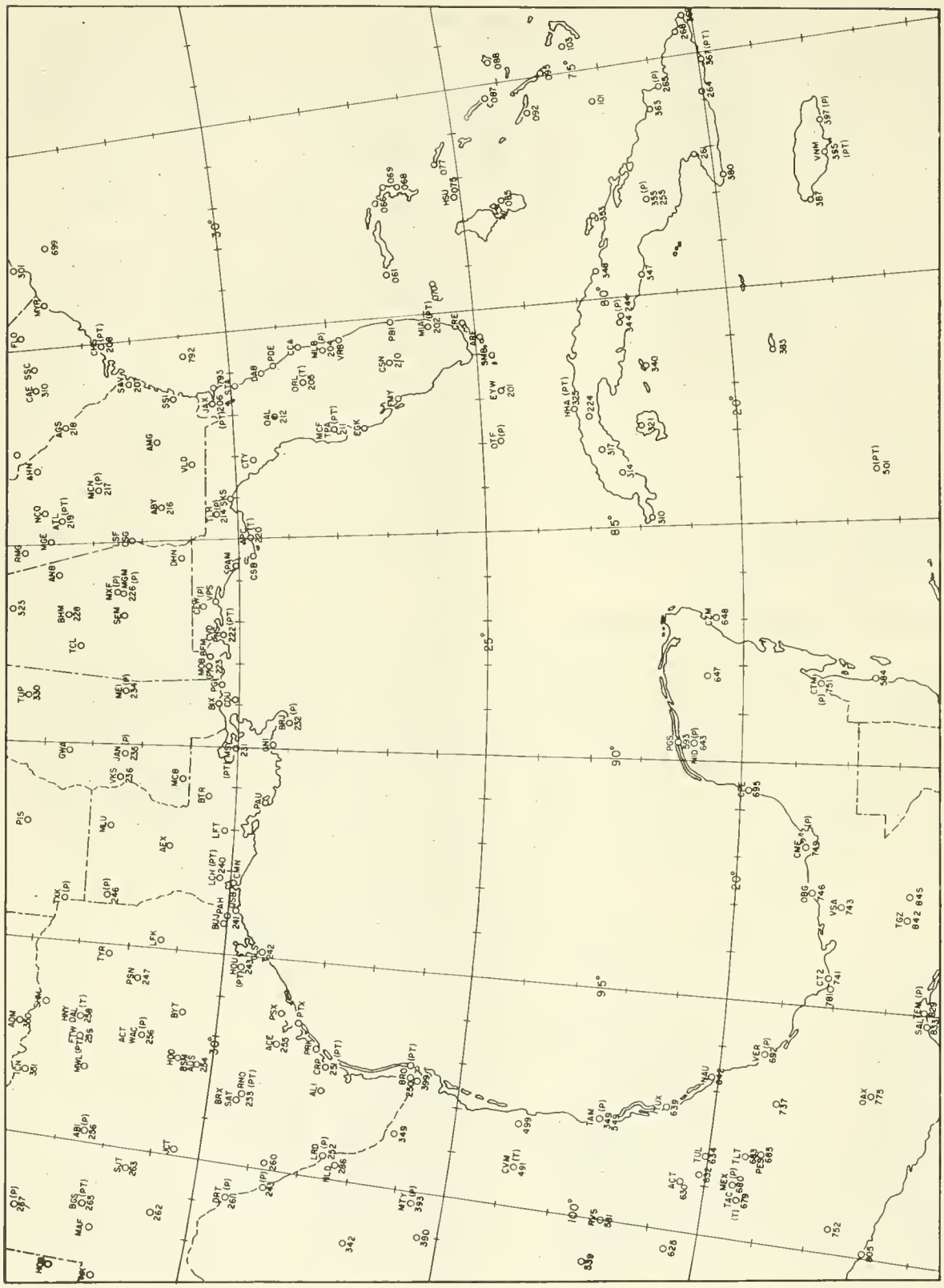

FIGURE 20.—Weather observing stations, Gulf of Mexico area.

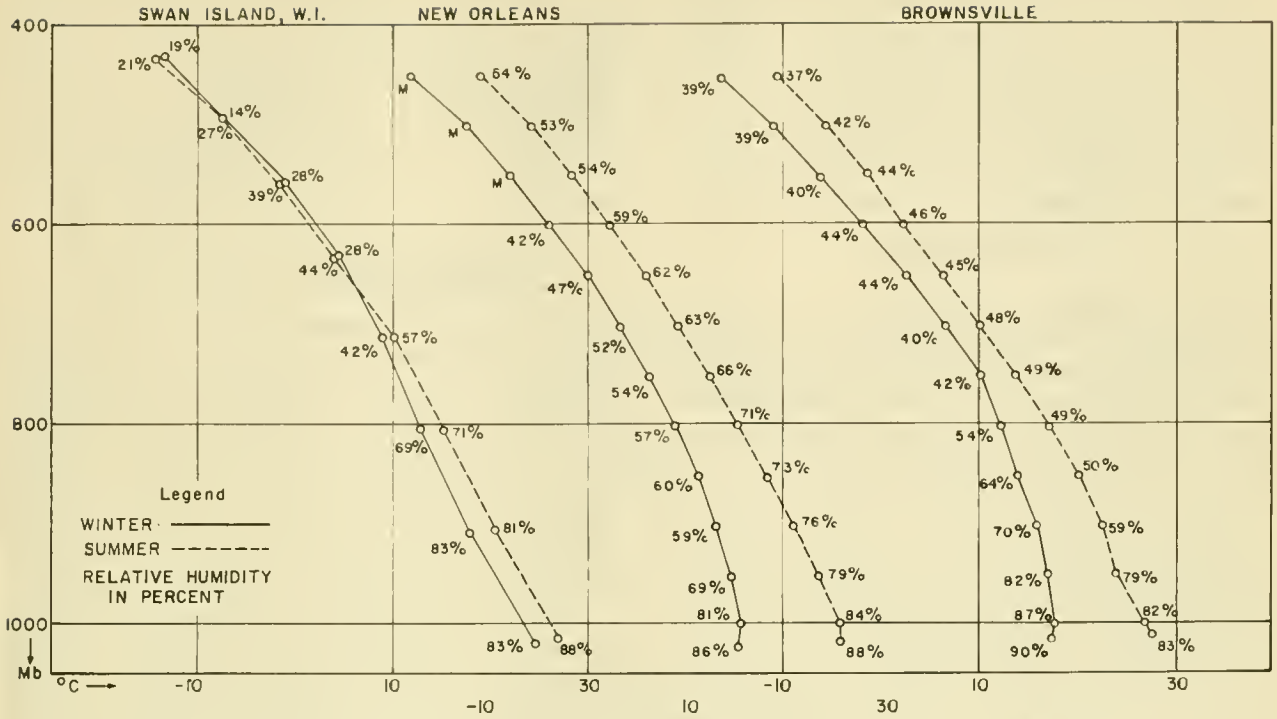

FIGURE 21.—Average radiosonde observations from selected stations in the Gulf of Mexico area.

(1951) demonstrated the modifying effects of the sea surface. He was able to support the usually assumed logarithmic distribution of water vapor with height, the variation of the evaporation coefficient with wind speed and the essential similarity of the heat and moisture transfer processes.

A discussion of the extent to which the sea surface affects the overlying atmosphere is given by Jacobs (1951). He computes the average winter evaporation in the Gulf to be of the order of 0.40 gms. per cm^2/day and compares this with the other ocean areas of the world. Similar comparisons are made for the other energy exchange processes operating between the sea and the atmosphere.

NORTHERS

A period of north winds lasting from 1 to 3 or 4 days and having speeds greater than approximately 20 knots is known to seamen as a "norther." Each year 15 or 20 northers are observed in the Gulf, usually between November and March. Many of them reach as far south as Key West, Florida, and Tehuantepec, Mexico. The low temperatures of the polar air masses which move in and the large waves built up in the open Gulf have considerable effect upon shipping and work at sea. Also, the water level is often lowered in the shipping canals and in harbors along the north coast markedly affecting ship transportation in the area. According to the Coast Pilot a veering of the north winds into the east and southeast brings a resumption of fair weather, while a backing toward northwest means more foul weather.

METEOROLOGICAL TIDES

Water levels along the coasts of the Gulf change noticeably with changes in wind speed and direction. Two extreme conditions are the change associated with a norther, mentioned above, and the storm tide associated with a hurricane and discussed later. However, the stress of the wind acting upon the sea surface at times other than times of northers or hurricanes may also be sufficient to bring about a water level change of the same order of magnitude as that resulting from the periodic tide-producing forces. This leads to considerable deviation of the observed water levels from those published in the tide prediction

manuals. It does not mean that the manuals are in error but rather means that a non-periodic, usually short-term wind effect must be superimposed upon the published predictions. One of the most challenging problems facing the meteorologist-oceanographer is that of finding a way to calculate these wind effects for different situations. Some work has been done by Dietrich (1937).

HURRICANES

The Galveston flood tide of 1900 in which 6,000 persons lost their lives emphasizes the impact of the Gulf coast hurricane upon that region. Much has been written on this and similar storms. Some references are the Coast Pilot, Tannehill (1944), Cline (1926, 1933), Riehl and Burgner (1950), and Shisler (1949).

Nearly 80 percent of the hurricanes appearing in the Gulf form outside and enter moving northwestward across the Yucatán Channel and Florida Peninsula area. Approximately 15 percent form in the northern Gulf, and most of the remainder form in the southwestern Gulf. They travel at an average speed of 10 to 13 knots. The most common path is westward becoming northwestward and northeastward. Some, however, do not turn northward. The months of greatest frequency and intensity are August, September, and October. There are an average of about nine hurricanes each year in the western North Atlantic, and many of these enter the Gulf.

Hurricanes are usually 100 to 500 miles in diameter. In the eye of the storm is a region of calm where the water level rises in a "hurricane wave" which may be 20 feet or more in height. Around the storm center, high-wind waves develop. Passing out of the wind area these waves become swells and often provide the first indication that a hurricane is approaching.

Much of the damage caused by hurricanes in coastal areas is due to the fact that the wind-driven storm tide raises the water level sufficiently that the high breaking wind waves are carried across breakwaters and retaining walls into unprotected inshore areas. The tracks of the centers of hurricanes which caused the highest tides of record on the Gulf coast are shown in figure 22. A detailed discussion of such meteorological tides is given by Cline (1933).

In recent years much has been learned about the formation and motion of hurricanes from the weather flights into the centers of the storms made by the United States Navy and other flights made by the Air Force. In addition, the storms have been followed by radar sets, since they make a distinctive pattern on the radar screen.

APPLICATIONS OF MARINE METEOROLOGY IN THE GULF

The heavy investments by the petroleum industry in the shallow waters of the Gulf (some 250 million dollars) are greatly affected by meteorological conditions as evidenced, for example, by a symposium on this and related subjects appearing in the February 23, 1950, issue of the Oil and Gas Journal. Glenn (1950) discusses the place of meteorologists in improving the safety and efficiency of offshore petroleum operations.

The many large industrial organizations on the coast need information about offshore weather for use in conducting their operations. Several organizations have established weather observation stations including radar facilities, such as those described by Jorgensen and Gerdes (1951).

Fishing here, as elsewhere, is successful or not depending to a large extent upon the weather. Navigation, protection of beaches, construction along the coast, and recreation all furnish applications for knowledge gained in the study of marine meteorology.

FURTHER SOURCES OF INFORMATION

Many pertinent articles on marine meteorology are reproduced on the back of the Pilot Charts. An index to those between January 1946 and September 1950, inclusive, appears on the chart for November 1951. Some examples are: Cyclonic storms—October 1949, Fog—September 1946, Hurricanes and Tropical Disturbances—August 1946, 47, and 48, Northers—September 1949, 50, and 51, Line Squalls—March 1948, Northers—September 1947 and November 1948, Waterspouts—December 1948, and the Gulf Stream—August 1950. These charts may be obtained for 30 cents each by addressing a request to the United States Navy Hydrographic Office, Washington 25, D. C.

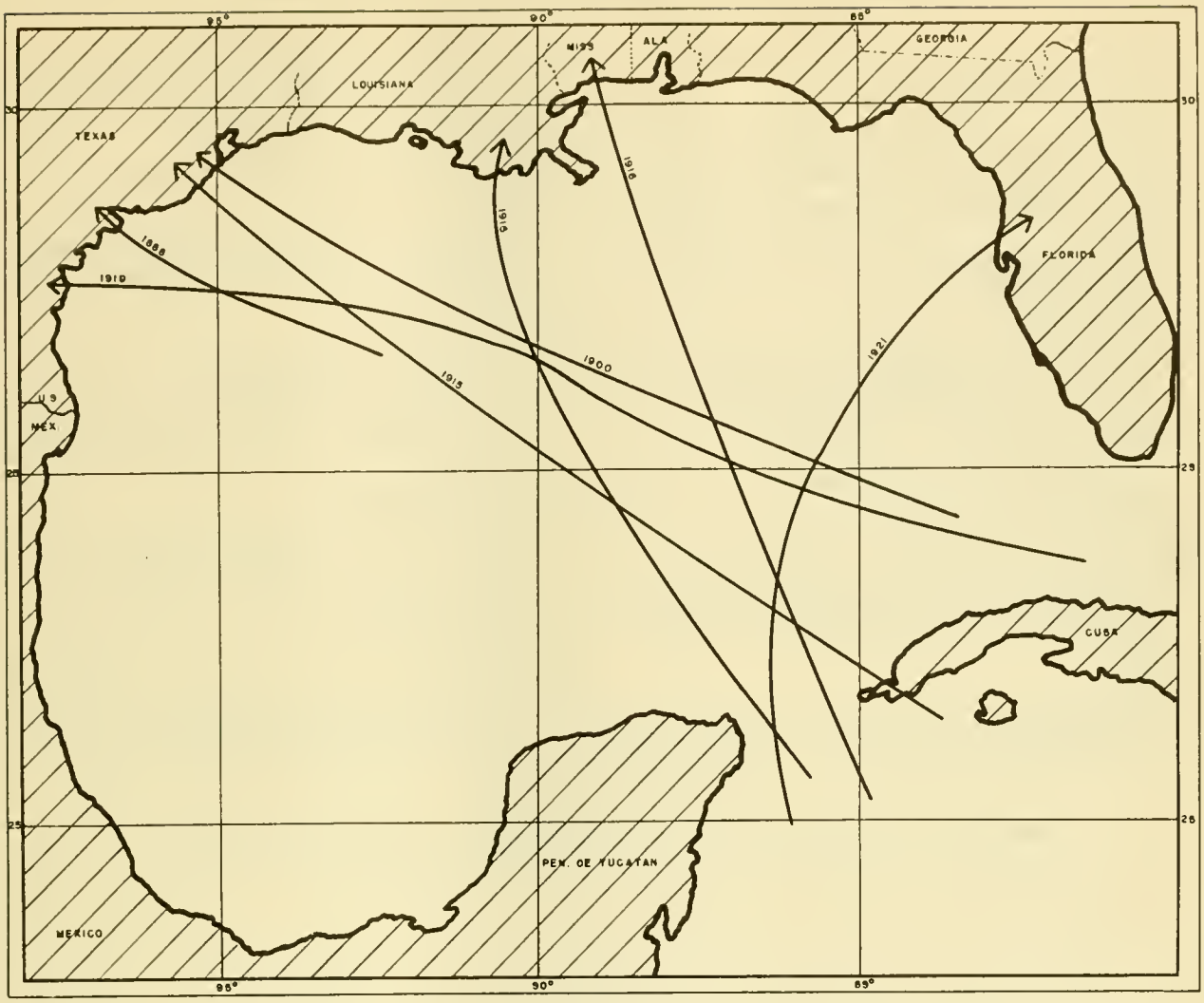

FIGURE 22.—Tracks of centers of hurricanes which caused highest tides of record on the Gulf coast. (Tannehill).

Geyer (1950) includes a number of references to the marine meteorology of the Gulf.

CONCLUSION

The development of marine meteorology in the Gulf of Mexico and other ocean areas has been delayed by the lack of sufficient information about the underlying water surface which exerts a dominating influence upon the atmosphere. Only recently has there been increased emphasis upon the collection of this information and upon the analysis of the data in such a manner as to lead to more complete understanding of the processes of interaction between the sea and the atmosphere and their effect upon the weather.

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CHAPTER IV

PHYSICS AND CHEMISTRY OF GULF WATERS

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TIDES AND SEA LEVEL IN THE GULF OF MEXICO

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The feature of the tide that makes the most marked impression on the observer along the shores of tidal waters is that relating to the magnitude of rise and fall, or the range of the tide, and where the range is large the tide is indeed an impressive phenomenon, visualizing in striking fashion the ceaseless warfare between land and sea. Wide stretches of foreshore constitute the field of battle. At low water these are seemingly part of the land, but a few hours later, at high water, the invading tide claims them again for the sea.

In the Gulf of Mexico the tide exhibits no such impressive sights, for the range of tide here is small, being at most places not much more than a foot or two on the average; but what the tide lacks in impressiveness for the casual observer, it more than makes up in the variety and complexity of the phenomena it offers the investigator.

Since the Gulf of Mexico is an arm of the Atlantic it is natural to attempt to correlate the tides in the two bodies of water. Figure 23 shows the tide curves for three stations on the coast of Florida for the last 8 days of June 1948. Miami Beach is on the Atlantic coast, and Cedar Keys and Pensacola are on the Gulf coast. The vertical lines at the top of the figure indicate noon of each day. The horizontal line associated with each set of curves represents the average or mean level of the sea at each station for the 8-day period. The height of the tide at each station is shown, in feet, by the scale at the left and is reckoned from sea level.

Examining the curve for Miami Beach it is seen that high water and low water succeeded each other at intervals of about 6¼ hours so that in each tidal day (which has an average length of 24 hours and 50 minutes) there are two high waters and two low waters. The high waters rose approximately the same height above sea level as the low waters fell below it, and while the two high waters of a day, as also the two low waters, differed somewhat in height, the difference was relatively small as compared with the range of the tide which for the 8-day period averaged 2.0 feet.

At Cedar Keys, as the middle diagram shows, there were likewise two high and two low waters a day, but consecutive cycles of rise and fall differed considerably more than at Miami Beach. For example, from the first high water on the 23d to the first high water on the 24th the consecutive ranges, in feet, were as follows: 1.2, 2.3, 4.5, and 3.4. For that tidal day, therefore, the average range was 2.85 feet, but individual ranges varied from 58 percent above to 58 percent below that average value. The durations of rise and fall likewise varied considerably. On the first day they were, in hours, 5.0, 5.5, 7.7, and 6.4. For the succeeding days the differences in range and in duration diminish more or less regularly until on the last 2 days the characteristics of rise and fall at Cedar Keys are much the same as at Miami Beach.

Now it must be noted that the differences found in character of tide at the two places are in no way due to the disturbing effects of wind or weather. As will be seen later such disturbing effects do occur and result in modifying profoundly the normal features of rise and fall. The last 8 days of June 1948 were chosen for illustration precisely because of the freedom during this period of disturbing effects of wind and weather. The differences in the features of the tide at the two places for the 8-day period are due to differences in tidal character.

Examining now the tide curve for Pensacola, the difference from the other two tide curves that strikes one immediately is that at Pensacola there were but one high and one low water a day for 7 of the 8 days. In other words, the periods of rise or fall here are approximately 12 hours against 6 hours at the other two places.

Note.—H. A. Marmer died before this article was set in print. The proofs were corrected in the Division of Tides and Currents, U. S. Coast and Geodetic Survey.

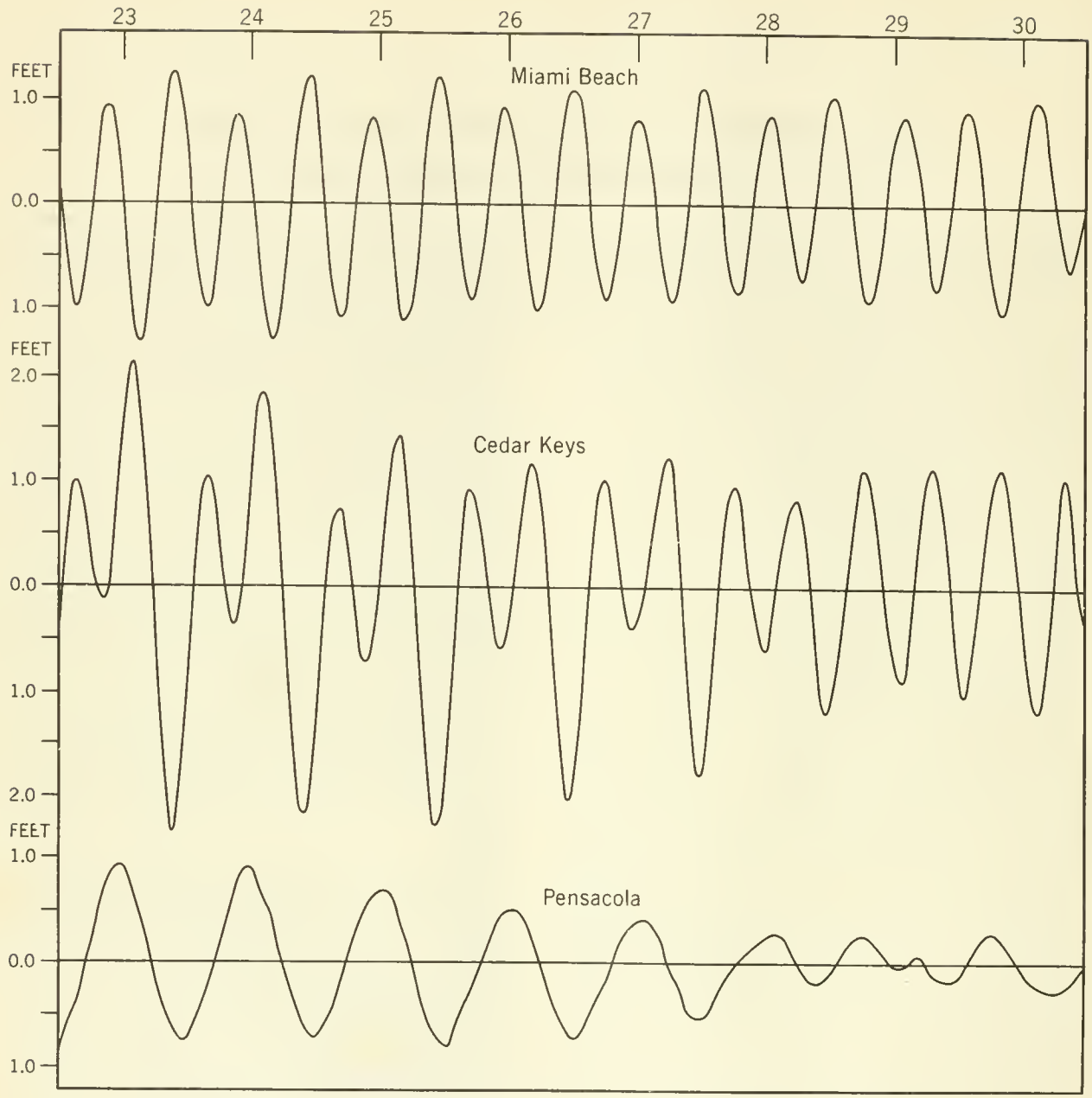

FIGURE 23.—Tide curves, Miami Beach, Cedar Keys, and Pensacola, June 23–30, 1948.

Pensacola is about 250 miles from Cedar Keys, and in this distance along the Gulf coast the tides differ strikingly. If we go up the Atlantic coast the same distance from Miami Beach, we find no such differences. In fact, in the 1,500-mile stretch from Florida to Maine, the characteristics of the tide along the Atlantic coast are much the same despite large differences in range of tide at different places. For example, at Bar Harbor, Maine, the mean range of the tide is 10.4 feet against 2.5 feet at Miami Beach. If we plot the tide curve at Bar Harbor for the last 8 days of June 1948 on a height scale one-fourth that at Miami Beach, the two tide curves would resemble each other closely.

To exemplify the character of the tide at other places in the Gulf of Mexico, we may take Key West, Florida, at the entrance to the Gulf, and Galveston, Texas, about 450 miles west of Pensa-

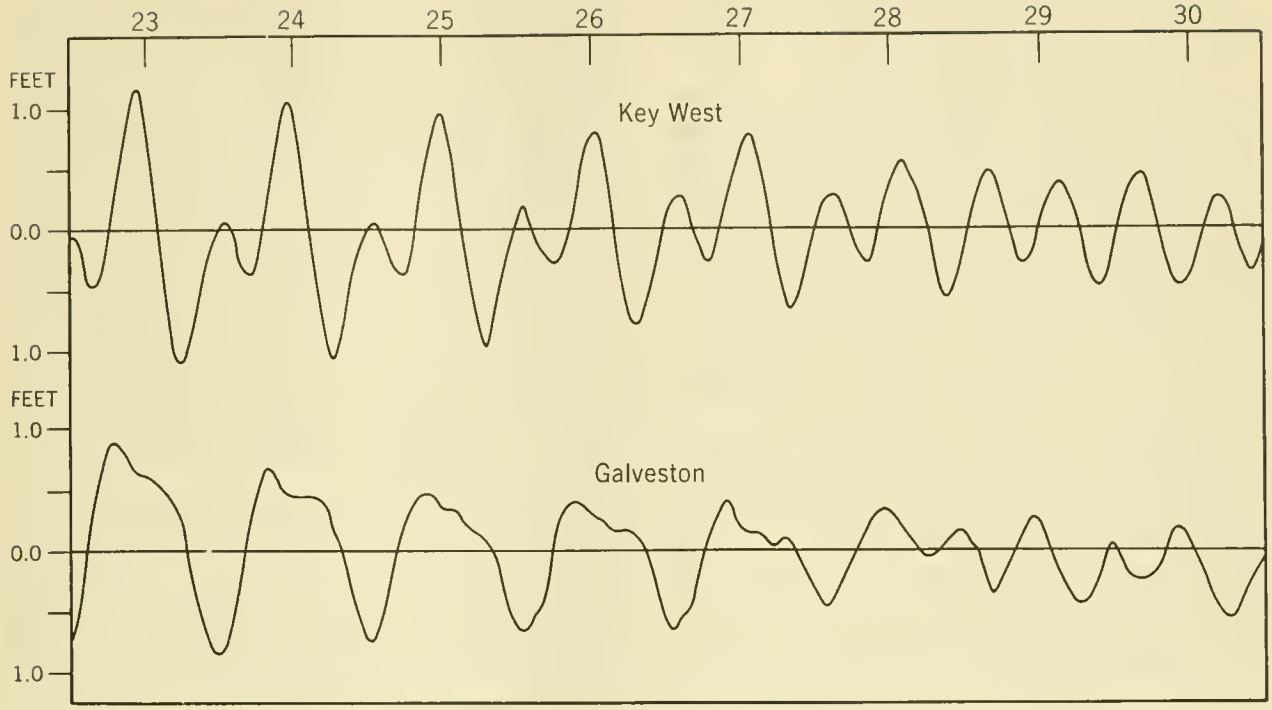

FIGURE 24.—Tide curves, Key West and Galveston, June 23–30, 1948.

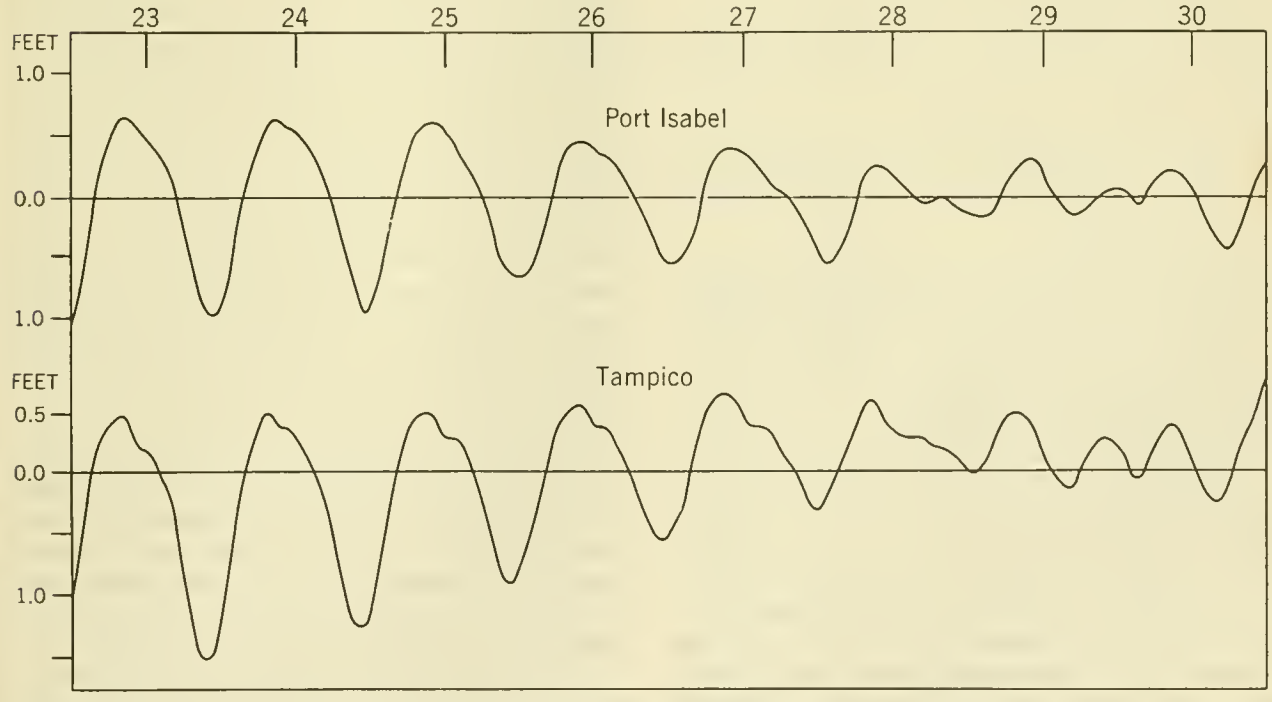

FIGURE 25.—Tide curves, Port Isabel and Tampico, June 23–30, 1948.

cola. In figure 24, are shown the tide curves for those two places for the same 8 days of June 1948 as in figure 23. The vertical lines at the top of figure 23 indicate noon of each day.

Compared to the two Gulf coast stations shown in figure 23 the tide curve at Key West resembles that at Cedar Keys more than that at Pensacola. Nevertheless, there are differences apart from that of range. At Cedar Keys the differences between the two low waters of a day are larger than those between the high waters, while at Key West the case is reversed. In fact, it will be noted in figure 24 that the lower high water at the beginning of the curve for Key West did not rise to the height of sea level.

At Galveston for the first 4 days there was only one high and one low water daily, as at Pensacola, but the fall from high water during these days was different in character from that at Pensacola, and the period of two tides a day began several days earlier than at Pensacola.

We may take the record at Port Isabel, Texas, and at Tampico, Mexico, to exemplify the tide on the western shore of the Gulf. The tide curves at the two places for the last 8 days of June 1948 are shown in figure 25. The vertical lines at the top of the figure indicate noon of each day.

At Port Isabel the tide curve resembles that at Pensacola closely except that at the latter place there was only 1 day with two high and two low waters, while at Port Isabel there were 3 days during which two high and two low waters occurred. At Tampico the tide curve appears to be about halfway between the tides at Galveston and at Port Isabel.

To complete the circuit of the Gulf we may discuss the tide at Coatzacoalcos and Progreso, Mexico, on the south shore and at Habana, Cuba, at the southeastern entrance. These are shown in figure 26 for the last 8 days of June 1948. As in figures 23–25, the vertical lines at the top of the figure indicate noon of each day.

At both Coatzacoalcos and Progreso the tide resembles that at Tampico, but at Habana the tide curve resembles most nearly that at Key West (fig. 24) except that the differences between the two high waters of the day are more intensified.

In the cursory examination of the tide for several days at 10 stations along the shores of the Gulf we have found very decided differences even though we have disregarded differences in range of tide. Differences in range of tide may be regarded as differences of degree rather than of kind. The differences we have found are of a more profound character than differences in range; they are differences of kind. Moreover, it must be borne in mind that at any place the tide changes in range from day to day, from month to month, and from year to year, and as our examination of the 8 days illustrated in figures 23 to 26 discloses, the character of rise and fall changes from day to day also. These changes in range and character of tide arise primarily from the changing positions of the moon with relation to earth and sun, but if we attempt to correlate these changes with the position of the moon we find the tides at the different places responding in different fashion.

Hence, if we are to avoid describing the tide at any place by detailed exposition of numerous changing features, we must make use of some clarifying concept which will bring the various tidal features into genetic relationship. Such a clarification is furnished by the concept of type of tide through the use of harmonic constants.

HARMONIC CONSTANTS

The tide-producing forces of sun and moon change from day to day in accordance with the changing positions of those bodies relative to the earth, but by mathematical analysis the tide-producing forces can be resolved into a number of simple periodic forces each having a fixed period. In other words, with regard to the tide-producing forces we may conceive the actual sun and moon with their complicated movements relative to the earth to be replaced by a number of hypothetical tide-producing bodies. These hypothetical tide-producing bodies are conceived as moving in circular orbits about the earth in the plane of the equator and each bringing forth a constituent tide of its own period.

The periods of these hypothetical tide-producing bodies can be calculated with precision from astronomical data. Hence, the actual tide at any place may be conceived as being made up of a number of constituent or component tides, each with a fixed period or speed corresponding to its appropriate hypothetical tide-producing body.

Analysis shows that the principal lunar component has a period of $12^h\ 25^m$ or an angular speed of 28.98° per hour. It is designated by the

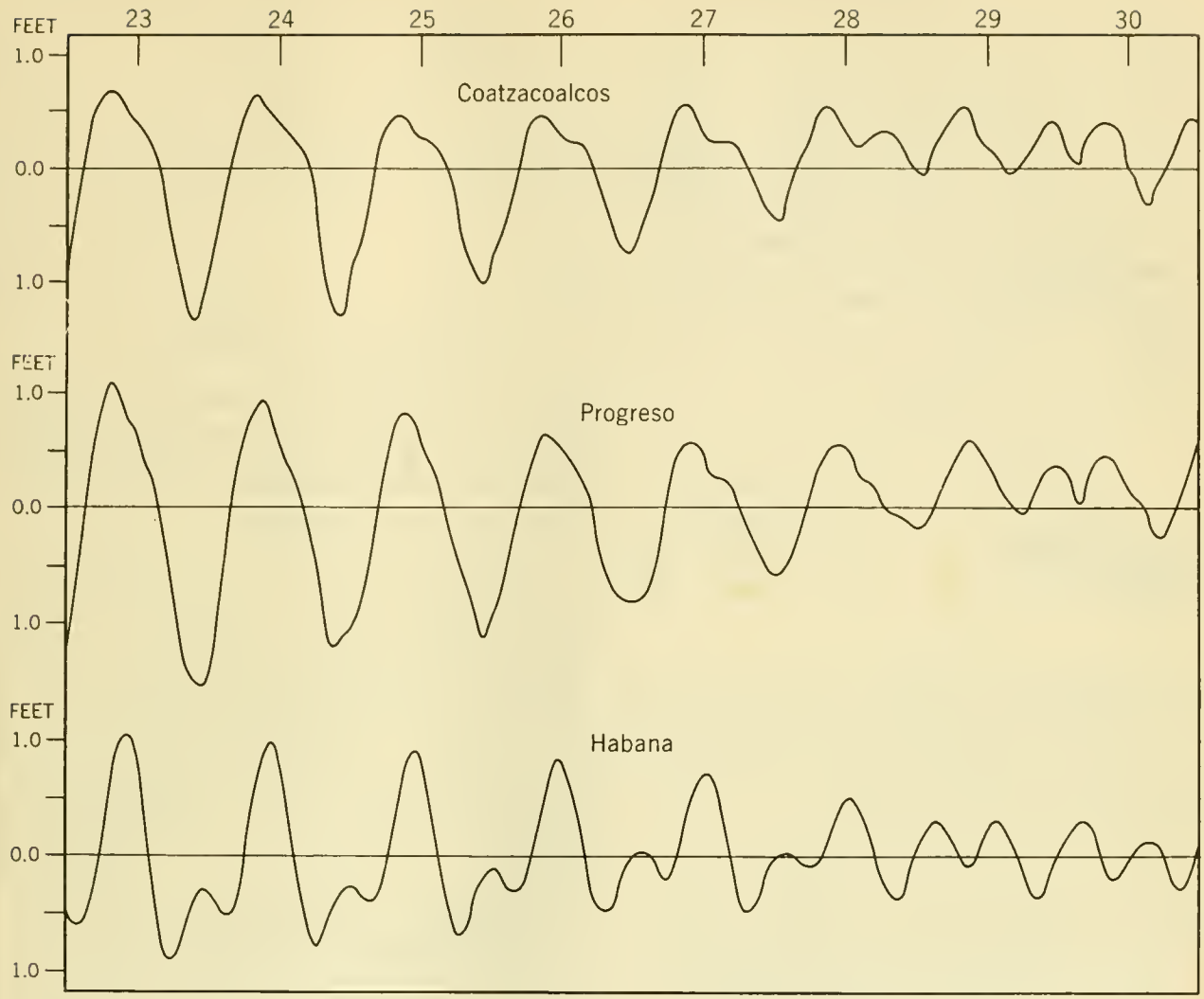

FIGURE 26.—Tide curves at Coatzacoalcos, Progreso, and Habana, June 23–30, 1948.

symbol M_2, the M indicating that it is a component derived from the moon's motion and the subscript 2 indicating that it is a semidiurnal component, that is, its period is half a day. The principal solar component has a period of exactly 12 hours and therefore an angular speed of 30.00° per hour. It is symbolized by S_2.

The actual moon does not move in a circular orbit but in an elliptical one. This means that its distance from the earth is not constant, and hence its tide-producing force varies, being less than average at apogee and greater at perigee, the period from one perigee to another being on the average, 27½ days. Analysis shows that for this reason it is necessary to introduce a simple component with a period of 12.66 hours or a speed of 28.44° per hour. It is designated as N_2 and is known as the larger lunar elliptic semidiurnal component.

Still another prominent feature of the relative movements of sun and moon with respect to the earth must be taken into consideration, namely, the fact that the planes of their orbits are inclined to the plane of the equator. This means that the declinations of sun and moon are constantly changing. It is found that two components must be introduced, symbolized by K_1 and O_1, the former arising from both the sun's and moon's tide-producing forces and called the luni-solar diurnal component and the latter arising from the moon's tide-producing force and called the lunar diurnal component.

Theoretically, the number of components is very large, but most of them are of such small magnitude that for general purposes they may be disregarded. Even in the prediction of tides by the use of tide-predicting machines it is rarely necessary to take into account more than 30 components. For an understanding of the principal features of the tide at any place the five principal components described above are sufficient.

The component tides are usually referred to as harmonic components, and for convenience the five principal harmonic components are listed in table 1.

TABLE 1.—*Principal harmonic components of the tide*

Name of component	Symbols	Speed per hour	Period
		Degrees	*Hours*
Principal lunar semidiurnal	M_2	28.98	12.42
Principal solar semidiurnal	S_2	30.00	12.00
Larger lunar elliptic semidiurnal	N_2	28.44	12.66
Luni-solar diurnal	K_1	15.04	23.93
Lunar diurnal	O_1	13.94	25.82

By subjecting the tide observations at any place to the harmonic analysis the amplitudes and epochs of the harmonic components at that place are determined. Collectively, the amplitudes and epochs of the component tides at any place are called the harmonic constants.

Of the five principal harmonic components listed in table 1 three have periods of about 12 hours, while the remaining two have periods of about 24 hours. All components with periods of about 12 hours are called semidiurnal or semidaily components, while those with periods of about 24 hours are called diurnal or daily components.

Any component tide is represented by the cosine curve and is completely specified by two characteristics, namely, the amplitude and the epoch. Figure 27 represents a component tide. The amplitude is the maximum ordinate represented by BE or FC; hence, the amplitude of a component tide is half the range of that tide. The epoch is the time, in angular measure, elapsing between the meridian passage of a hypothetical tide-producing body and the high water of its tide. In figure 27, the curve ABCD represents the rise and fall of a component tide for a complete period, A being the instant of meridian passage of the particular hypothetical tide-producing body considered. The height of this component tide at any instant is measured vertically up or down

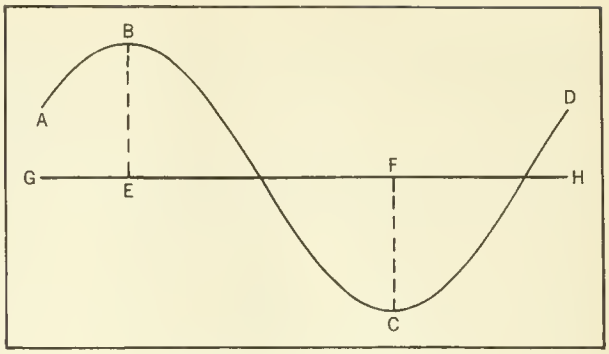

FIGURE 27.—Component tide.

from the line GH which represents the undisturbed sea level, while the time is measured along this line from G to H. Hence, the distance GE expressed as an angle, which is (GE÷GH) 360°, is the epoch of the component.

In this connection it should be noted that the tide-producing forces depend on the relative positions of earth, moon, and sun. Hence, at any given instant the tide-producing forces are distributed over the earth in a regular manner varying with longitude and latitude. But the response of the different seas to the same set of tide-producing forces is so profoundly modified by the hydrographic features of the different oceanic basins that the tides at different places differ profoundly. To understand the use of harmonic constants in determining types of tide, it will be of advantage to consider briefly the combination of component tides.

Suppose that at a given place conditions are such as to bring about a daily and a semidaily component of the same range. What is the nature of the resulting tide?

Obviously the two constituents may have various time or phase relations. In figure 28, three cases are considered. The semidaily constituent is represented by a dotted curve; the daily constituent by a dashed curve. The height of the resultant tide at any moment is clearly the sum of the heights of the constituent tides at that moment. In the figure the resultant tide is indicated by the full line curve.

In the upper diagram of figure 28, the two constituents have such time relations that their low waters occur at the same time, and the resultant tide is one in which the inequality in morning and afternoon tides is featured in the low waters and is exemplified by the tide at Cedar Keys on August

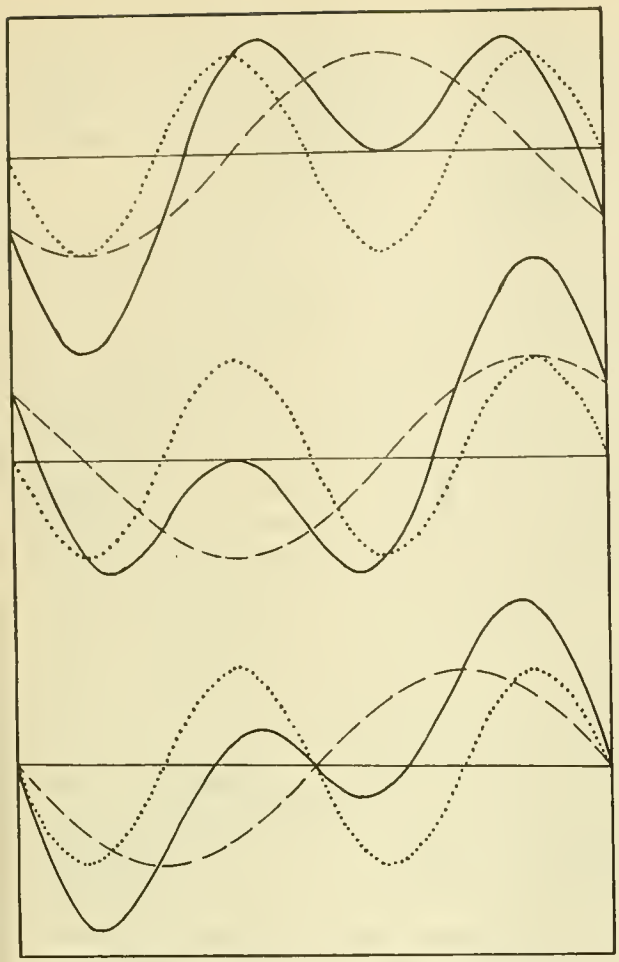

FIGURE 28.—Combination of daily and semidaily constituent tides with equal ranges.

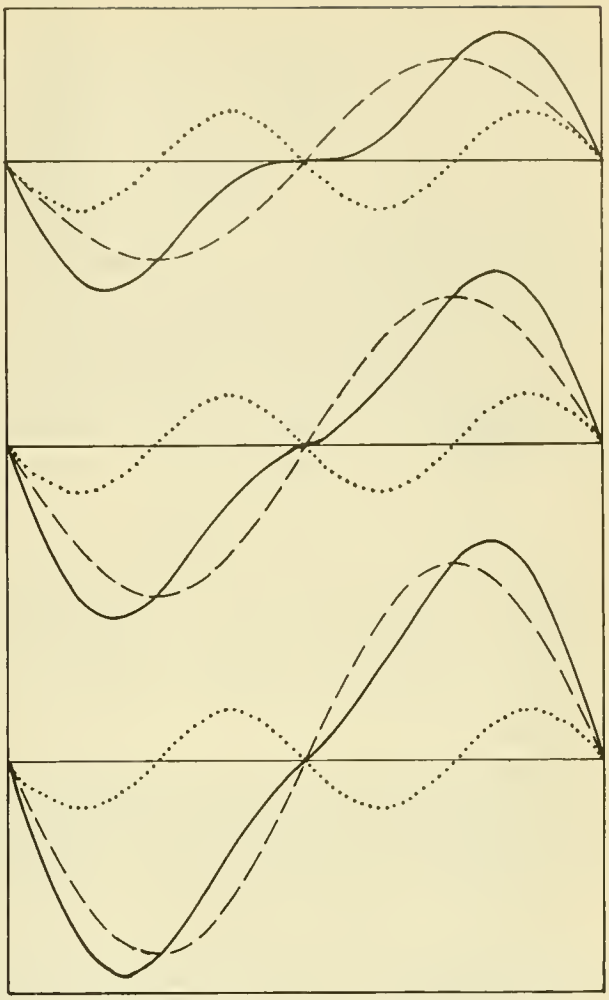

FIGURE 29.—Combination of semidaily and daily constituent tides with different ranges.

26 to 29 in figure 23. The middle diagram represents the case in which the high waters of the two constituents occur at the same time, the resultant tide featuring the inequality in the high waters. The lower diagram represents the condition when the two constituents are at sea level at the same time. The inequality is now distributed equally in the high and the low waters, exemplified by the tide at Key West on August 26 and 27 in figure 24.

Thus far, we have considered only the combination of component tides of equal ranges. What is the character of the tide resulting from the combination of daily and semidaily components of unequal ranges?

In figure 29, three cases are considered, the time or phase relations between the two constituents remaining the same, the two constituents being taken so that they are at sea level at the same instant. In the upper diagram of figure 29, the daily constituent is taken with a range twice that of the semidaily, in the middle diagram the ratio is 3 to 1 and in the lower diagram 4 to 1. With a ratio of 2 to 1, the upper diagram shows the resultant tide to be one with but one high and one low water but featuring a relatively long stand halfway between high and low water. With increasing ratios, that is with relatively larger daily constituents, the stand becomes shorter and shorter as the middle and lower diagrams show. With a ratio of 4 to 1 the resultant curve approximates the shape of the daily constituent.

If in figure 29 the time relations between the two components were taken differently, the shapes of the resultant tides would be somewhat different. Without going into further detail it is clear that

where the daily constituent is less than twice that of the semidaily, the resultant tide will exhibit two high and two low waters a day with the inequality in the tides depending on the phase relations between the constituents. When the ratio is between 2 and 4 the resultant tide will have either two high and two low waters a day or only one high and one low water depending on the phase relations between the two constituents. When the ratio is 4 to 1 or greater, there will be only one high water and one low water a day.

With this brief discussion of harmonic constants and the combination of constituent tides, admittedly sketchy, we are in a position to discuss types of tide.

TYPES OF TIDES

The great variety of tides found throughout the world can be grouped under three large classes or types: semidaily, daily, and mixed. The idealized forms for these different types are furnished by the component tides and their combinations.

The semidaily type of tide includes all those in which the tidal cycle is completed in half a day; that is, there are two high and two low waters a day with only little difference between corresponding morning and afternoon tides.

The daily type of tide includes tides in which only one high and one low water occur in a day. The mixed type of tide includes those tides which feature two high and two low waters a day but with considerable difference between the two high waters and/or between the two low waters of the day.

It is to be noted that when the tide at any place is classed with a particular type in accordance with the above definitions, it is the generally prevailing or predominating features that are considered. For example, in figure 23 the tide at Miami would be designated as the semidaily type, although for a few days each fortnight, morning and afternoon tides exhibit some inequality. In the same way the tide at Cedar Keys would be classed with the mixed tides, although as the last 2 days of figure 23 show, but little inequality was featured by the tide. Pensacola would be classed with the daily tide because for the greater part of the time but one high and one low water a day occur.

For general purposes, the definitions of the three types of tide given above are sufficient, but it is clear that these definitions do not provide sharp distinctions between the three types. For technical purposes, definite criteria may be determined through the use of harmonic constants.

Of the five principal harmonic constituents listed in table 1, K_1 and O_1 represent the principal daily components, while M_2 and S_2 represent the principal semidaily components. The ratio of K_1+O_1 to M_2+S_2 at any place therefore defines the relative magnitudes of the principal daily and semidaily components at that place. Van der Stok (1897) suggested the use of these ratios for classifying types of tides. Where $(K_1+O_1)\div(M_2+S_2)$ is less than 0.25 the tide is classed as semidaily; where it is between 0.25 and 1.50 it is classed as the mixed type; and where it is greater than 1.50 it is classed with the daily type.

The diurnal type of tide under the above classification is found to cover a great variety of tides, from those only infrequently diurnal to those predominantly diurnal. In recent years it has been suggested (Courtier 1938) that the diurnal type be separated into two types: (1) mixed diurnal, where the ratio is between 1.5 and 3; (2) diurnal, where the ratio is greater than 3. The term "mixed diurnal," in turn, suggests mixed semidiurnal as a better designation than mixed.

For convenience, the four types of tide and the corresponding ratios of K_1+O_1 to M_2+S_2 are given in tabular form in table 2. It should be noted that the terms semidaily and semidiurnal are used as synonymous and likewise the terms daily and diurnal.

TABLE 2.—*Types of tide*

Designation	$(K_1+O_1)\div(M_2+S_2)$
Semidiurnal or semidaily	0–0.25
Mixed semidiurnal or mixed semidaily	0.25–1.50
Mixed diurnal or mixed daily	1.50–3.00
Diurnal or daily	3.00

The harmonic constants of the tide at any place are derived from tide observations at that place by means of the harmonic analysis. For a precise determination of these constants, a year of observations is desirable, but shorter series of observations will furnish dependable results. The harmonic analysis is a highly specialized process, which need not be considered here. For a detailed discussion see Manual of Harmonic Analysis

and Predictions of Tides, by Paul Schureman (1940). It will be sufficient for our purposes to indicate the use of these constants in determining types of tide and in deriving tidal characteristics. Table 3 gives the four principal harmonic constants at the tide stations in the Gulf of Mexico where they have been determined. The amplitude of component N_2 throughout the Gulf is small, generally less than 0.1 foot, and is therefore not included in the table.

TABLE 3.—*Harmonic constants, Gulf of Mexico*

Station	Lat. North		Long. West		K_1		O_1		M_2		S_2		$\frac{K_1+O_1}{M_2+S_2}$	Observations	
					Amp.	G	Amp.	G	Amp.	G	Amp.	G		Year	Length
FLORIDA	°	′	°	′	*Feet*	*Deg.*	*Feet*	*Deg.*	*Feet*	*Deg.*	*Feet*	*Deg.*			
Key West (north shore)	24	34	81	48	0.28	361	0.29	357	0.55	77	0.17	101	0.79	1914	1 year.
Key West (west shore)	24	33	81	48	.29	358	.29	354	.56	71	.17	93	.79	1939	Do.
Garden Key	24	38	82	52	.37	358	.36	354	.48	84	.12	97	1.22	1860	Do.
Everglades, Barron River	25	51	81	23	.30	74	.26	67	.78	239	.22	265	0.56	1929	Do.
Naples	26	8	81	48	.50	11	.44	4	.89	143	.30	157	.79	1933–34	Do.
South Boca Grande	26	43	82	15	.41	28	.37	20	.37	150	.13	156	1.56	1933–34	Do.
Anna Maria	27	32	82	44	.48	23	.47	12	.51	134	.20	146	1.34	1933–34	Do.
St. Petersburg	27	46	82	38	.52	50	.50	40	.55	201	.19	218	1.38	1925–26	Do.
Aripeka	28	27	82	40	.53	48	.51	38	.88	191	.32	226	0.87	1933–34	Do.
Cedar Keys	29	8	83	2	.55	39	.47	29	1.07	190	.38	216	.70	1939	Do.
St. Marks Light	30	4	84	11	.56	37	.52	30	1.04	205	.43	231	.73	1933–34	Do.
Warrington	30	21	87	16	.41	47	.41	37	0.06	132	.03	130	9.11	1859	Do.
Pensacola	30	24	87	13	.44	56	.42	47	.07	173	.02	179	9.56	1939	Do.
ALABAMA															
Mobile Point Light	30	14	88	1	.38	46	.37	36	.07	117	.03	129	7.50	1850–51	Do.
Mobile	30	41	88	2	.47	80	.46	68	.05	212	.04	254	10.33	1934	Do.
MISSISSIPPI															
Biloxi	30	24	88	51	.57	48	.51	38	.11	189	.09	209	5.40	1882	Do.
Cat Island	30	14	89	10	.52	54	.48	44	.12	189	.07	202	5.26	1848	Do.
LOUISIANA															
New Orleans, Lake Pontchartrain	30	1	90	7	.09	199	.09	190	.01	60	.01	120	9.00	1898	58 days.
Pass Manchac Light, Lake Pontchartrain	30	18	90	18	.07	197	.08	199	.00	------	.01	106	15.00	1897	105 days.
New Orleans, Mississippi River	29	55	90	4	.25	101	.26	89	.02	239	.02	256	12.75	1940–41	221 days.
Port Eads, Mississippi River	29	1	89	10	.39	20	.39	11	.06	118	.04	113	7.80	1940–41	Do.
Bayou Rigaud	29	16	89	58	.32	47	.32	40	.04	169	.02	338	10.67	1948–49	1 year.
Weeks Bay	29	48	91	50	.32	105	.30	92	.16	9	.05	348	2.95	1906	Do.
Eugene Island	29	22	91	23	.56	33	.46	29	.30	253	.12	252	2.43	1941	Do.
Calcasieu Light	29	47	93	21	.46	25	.42	14	.52	259	.18	254	1.26	1933–34	Do.
TEXAS															
South Jetty Light	29	20	94	42	.49	33	.49	24	.45	276	.15	272	1.63	1936–37	Do.
Fort Point	29	20	94	46	.39	50	.36	44	.31	297	.09	301	1.88	1903–04	Do.
Galveston, Galveston Bay	29	19	94	48	.38	51	.36	42	.31	301	.10	302	1.80	1939	Do.
Gilchrist, East Bay	29	31	94	30	.26	105	.27	101	.20	37	.07	35	1.96	1936–37	Do.
Round Point, Trinity Bay	29	45	94	42	.22	134	.25	119	.13	72	.02	56	3.13	1936–37	Do.
Morgans Point	29	41	94	59	.24	139	.25	123	.09	88	.03	79	4.08	1936–37	Do.
Carancahua Reef, West Bay	29	13	95	0	.25	99	.26	88	.14	27	.04	26	2.83	1936–37	Do.
Rockport	28	1	97	3	.06	103	.06	91	.02	329	.00	------	6.00	1938	Do.
Port Isabel	26	4	97	13	.35	44	.35	35	.17	280	.04	292	3.33	1946	Do.
MEXICO															
Tampico	22	15	97	51	.43	24	.43	21	.23	250	.07	257	2.87	1942–43	Do.
Veracruz	19	12	96	8	.54	18	.63	56	.20	267	.07	187	4.33	1857	87 days.
Coatzacoalcos	18	9	94	25	.45	25	.45	19	.25	244	.07	246	2.81	1946–47	1 year.
Campeche	19	50	90	32	.87	44	.60	30	.72	271	.22	298	1.56	1900	105 days.
Progreso	21	17	89	40	.58	30	.56	21	.20	271	.06	280	4.38	1946–47	1 year.
CUBA															
Habana	23	9	82	20	.31	9	.33	5	.42	46	.14	70	1.14	1947	Do.

It will be recalled that two characteristics define or determine a given component tide, namely, the amplitude and phase or the epoch as the latter is generally called with reference to tides. Formerly, it was customary to refer the epoch to the local meridian and to designate it by the Greek letter "kappa." However, in comparing phases at different places it is more convenient to use a single meridian for reference, and the meridian of Greenwich is used for this purpose, the phase being designated by G. In table 3 the phases are all referred to the meridian of Greenwich. The stations in the table are listed in order beginning at the eastern end of the northern shore of the Gulf and continuing around the periphery counterclockwise. For several of the stations listed harmonic constants are available for several series of observations in different years. In such cases, the results from the latest year are given in the table.

For comparison with the tides in the Gulf it will be of interest to have the ratio of K_1+O_1 to M_2+S_2 for Miami Beach, on the Atlantic coast of Florida, for which place the tide curve is shown in figure 23. For Miami Beach this ratio is 0.17, and by the criteria of table 2 the tide there is of the semidaily type. From the last column of table 3 it is seen that at no place in the Gulf does this ratio fall below 0.5 so that in the Gulf the semidaily type is not represented.

From Key West to St. Marks Light the ratio is seen to be greater than 0.25 but less than 1.50 except for South Boca Grande. Hence, the tide in this stretch is of the mixed semidaily type. From Warrington to Bayou Rigaud the ratio is greater than 3, and therefore in this stretch the tide is of the daily type. From Weeks Bay around the remainder of the periphery of the Gulf to Habana the ratio fluctuates between 1.5 and 6 except for Calcasieu Light where it is 1.26 and for Habana where it is 1.14 so that the tide in this stretch varies from mixed diurnal to diurnal with only few exceptions.

The classification of the tide into types is of great convenience in tidal investigation, for as soon as the tide at any place is particularized as to type we are in possession of guiding principles for the discussion of the tide at that place. It will therefore be of advantage to summarize briefly the characteristic features of the different types of tide.

SEMIDAILY TYPE

The distinguishing feature of the semidaily type of tide is the occurrence of two high waters and two low waters in the tidal day (which has an average length of $24^h\ 50^m$) with relatively little difference between corresponding morning and afternoon tides. High waters succeed each other at intervals of about 12½ hours, and likewise the low waters.

The predominant change in range in the semidaily type of tide is that in response to the moon's phase, the greatest range, the so-called spring tides coming near the times of new and full moon, and the least range, the neap tides coming near the times of the moon's first and third quarters. The average interval between spring and neap tide is one-quarter the length of the month of the moon's phase (the synodic month), or approximately 7½ days. During this interval from springs to neaps the range of tide in the semidaily type of tide decreases from about 20 percent above the average to about 20 percent below the average; and in the next period from neaps to springs returns to 20 percent above the average or mean range.

Another prominent variation in the range of tide of the semidaily type is that in response to the moon's parallax which has a period averaging approximately 27½ days (the anomalistic month). Near the times of the moon's perigee the range of tide of the semidaily type is about 20 percent greater than average, while near the times of the moon's apogee the range is about 20 percent less than average. Obviously, therefore, at such times when the moon's perigee occurs near the times of new or full moon, the range of tide will be about 40 percent above the mean range, while at the times when the moon's apogee occurs near the times of the moon's quadratures the range will be about 40 percent less than the mean.

The third variation in range to which tides are subject is that in response to the moon's declination, which manifests itself in a difference between morning and afternoon tides, but is relatively small in the semidaily type of tide. In the moon's fortnightly change from maximum northerly to maximum southerly declination, the differences between morning and afternoon tides are greatest near the times of maximum declination and least about the times the moon is over the equator.

The range of tide is also subject to a slow change over a period of 18.6 years due to changes in the inclination of the moon's orbit to the equator. When the inclination of the orbit to the equator is at a maximum the semidiurnal range is less and when the inclination is at a minimum the semidiurnal range is greater than the 18.6 year-average. The change varies from about 3 percent below to 3 percent above average. The year 1950 corresponds to the year of minimum range, the year of the next maximum of this variation being 1959.

DAILY TYPE

The daily type of tide is characterized by the occurrence of only one high water and one low water the greater part of the time. The change from day to day in time of tide of this type is not nearly so regular as in the semidaily type in which the tide becomes later each day by about 50 min-

utes. In the daily type the average retardation in time likewise is 50 minutes, but from one day to the next it may vary from this average by several hours either way. This seeming irregularity in time is not due to chance effects, the tides of the daily type can be predicted quite accurately, but to the interaction of the component tides.

The most prominent variation in range of tide in the daily type is the fortnightly change associated with the moon's declination. When the moon is near its maximum semimonthly declination the range of tide in the daily type is greatest, the tides then being called tropic tides, and when the moon is over or close to the equator the tide has its least range, the tides then being called equatorial tides. This is exemplified for the tide at Pensacola by the lower curve of figure 23. For the latter part of June 1948 the moon was at its maximum southern declination on the 21st and over the equator on the 29th.

In general, it may be expected that in the diurnal type of tide, there will be several days around the time the moon is over the equator when two high waters and two low waters will occur, the larger the ratio of K_1+O_1 to M_2+S_2 the smaller the number of these days. These secondary tides pose troublesome questions in connection with the determination of the mean range of tide in tides of the diurnal type. Such secondary tides do not enter suddenly nor do they fade out suddenly. Practically, it becomes difficult to determine on a tide record whether the fluctuations are true secondary tides or fluctuations due to wind and weather. Furthermore, there is the question at what stage of development of these secondary tides shall they be included; when the range is 0.01 foot, 0.1 foot, or what?

To obviate these difficulties, it is customary to consider the diurnal tide as if it were diurnal at all times and in deriving the mean range to disregard the secondary tides. Thus, in figure 23 in the tide curve for Pensacola on the 29th, the secondary low water immediately after noon and the following secondary high water would be disregarded, and but one high water and one low water in the day would be considered. In determining mean high water and mean low water in tides of the diurnal type only one high water and one low water a day, likewise, are considered.

In figure 23, on June 23 when the moon was 2 days past its semimonthly maximum declination, the range of tide at Pensacola was 1.7 feet; on the 21st, the range was 1.9 feet. On the 29th, when the moon was over the equator the range (leaving the secondary tides out of consideration) was 0.5 foot. In the 8-day period, therefore, the range decreased 74 percent. This relatively large percentage change in range in response to the moon's declination is typical of daily tides.

At times, the terms "spring tides" and "neap tides" are used in connection with the fortnightly variation in range in the daily type discussed above, but this usage is confusing, the correct terms being tropic tides and equatorial tides. In the daily type of tide the variation in range with the moon's phases is so small that it may be disregarded for most purposes. The same remark applies to the variation in response to the moon's parallax, that is, apogean and perigean tides.

A variation in range of tide that is prominent in the daily type but not in the semidaily is of an annual period in response to the annual variation in the declination of the sun. This is illustrated in figure 30 by the results of the observations at

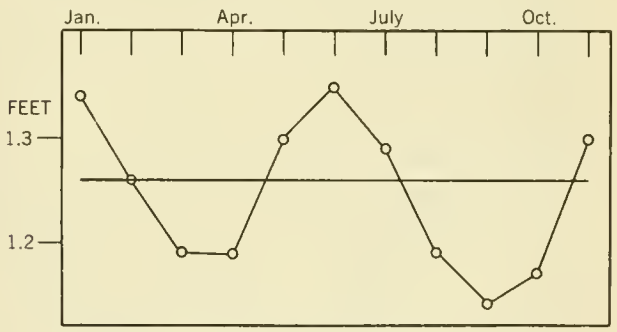

FIGURE 30.—Annual variation in range of tide, Pensacola.

Pensacola from the 19-year series 1931–49. The horizontal line, corresponding to the value of 1.26 feet, represents the mean value of the range at Pensacola, while the circles represent the average ranges for the different months of the year. During the year, the range is least in March and September, corresponding with the sun's equinox and greatest in June and December, corresponding to the sun's solstices, the difference between September and December being on the average 0.26 foot for Pensacola.

The range of tide in the daily type also is subject to a slow change of 18.6 years, due to changes in the inclination of the moon's orbit to the equator, as is the semidaily type, but is opposite in phase. During the years when the inclination of the orbit to the equator is greatest, the range in the semidaily type is less than the average, but in the daily type it is greater than the average, and during the years when the inclination is least, the range in the semidaily type is greater than the average while in the daily type it is less than the average. The results from 19 years of observations are shown in figure 31 for Miami Beach and Pensacola, illustrating the differences in the semidaily and daily types as regards this 19-year variation.

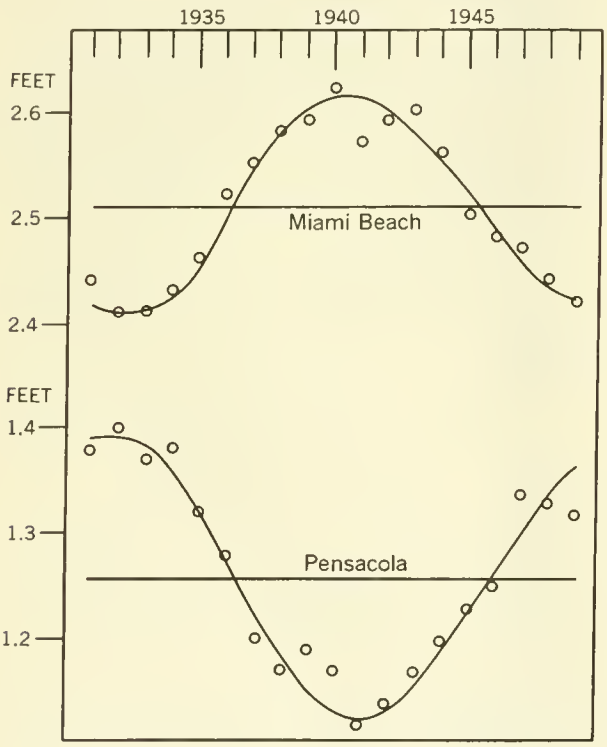

FIGURE 31.—Variation in yearly range of tide, Miami Beach and Pensacola.

The circles in figure 31 represent the yearly values of the range of the tide as derived from the continuous observations at the two stations, the more or less smooth curves being drawn to follow the yearly values with due consideration to the years of maxima and minima which are fixed from theoretical considerations. The deviations of the yearly values from the curves may be regarded as irregularities due to wind and weather.

For Miami, the change in range from the minimum in 1931–32 to the maximum in 1941 is 0.20 foot or 0.1 foot each way from the mean range which represents a change of 4 percent from the mean value of the range of 2.51 feet. For Pensacola, the change in range from the minimum to the maximum yearly value is 0.27 foot or 0.135 foot each way from the mean range which represents a change of 11 percent either way from the mean value of the range of 1.26 feet. In the daily type, therefore, the percentage change in the yearly range of tide is greater than in the semidaily type.

MIXED TYPES

From the preceding discussion of the semidaily and daily types it is clear that the mixed types of tide will vary in characteristics depending on the ratios of the semidaily and daily constituents. In the mixed semidaily type the diurnal inequality becomes a salient feature necessitating the differentiation between higher high water and lower high water and between higher low water and lower low water. The diurnal inequality, that is, the difference between the two high waters and the two low waters of a day will be greatest near the times of the moon's semimonthly maximum declinations and least when the moon is close to the equator. During the 19-year cycle there may be periods, in the years of maximum inclination of the moon's orbit, when the tide will become diurnal.

In the mixed daily tides there will be more days of the occurrence of two high waters and two low waters each fortnight near the times of the moon's crossing of the equator in the years of minimum inclination of the moon's orbit.

The changes from day to day in the features of the tide of the mixed types of tide are thus much more varied than in either of the simpler types. However, the tide tables permit the delineation of these changes from day to day. If the tide tables give the daily predictions for the place where this information is desired, the information is immediately available. Otherwise, it is necessary to infer the predictions from the predictions at some port with similar tides.

CHARACTERISTICS FROM HARMONIC CONSTANTS

From the harmonic constants formulae may be developed not only for determining the type of tide but also various characteristics of the tide. For precise results the formulae are rather involved and require other of the harmonic constants than those listed in table 3. For general purposes, however, simplified formulae are convenient for determining such characteristics approximately.

In the semidaily type of tide M_2 and S_2 are the principal components. Spring tides come when they conspire, and neap tides, when they are opposed. Hence, the formula 2.0 (M_2+S_2) gives an approximate value of the spring range, and 2.0 (M_2-S_2) gives an approximate value of the neap range. The mean range is given approximately by $2.2M_2$.

In the daily type of tide K_1 and O_1 are the principal constituents. When K_1 and O_1 conspire, tropic tides occur, and the formula for the tropic range, 2.0 (K_1+O_1), gives an approximation to the tropic range. The mean range for a daily type will be given approximately by 1.5 (K_1+O_1).

In the mixed types of tide things are more complicated, but the formulae for the ranges of the semidaily type may be used for the mixed semidaily, and the formulae for the daily tides may be used for the mixed diurnal.

In the discussion of the combination of component tides (p. 106), it was found that the phase relations between the daily and semidaily components determined whether the inequality would be featured principally in the high or low waters or equally in both. The following rule applies: If the difference between $M_2°$ and $(K_1°+O_1°)$ is zero, the inequality is wholly in the high waters; if the difference is 90°, the inequality is exhibited in equal degrees in both high and low waters; if the difference is 180°, the inequality is wholly in the low waters. In the application of this rule, the difference between $M_2°$ and $(K_1°+O_1°)$ is taken without reference to the sign of the result, and when this difference is greater than 180°, it is to be subtracted from 360°.

To exemplify the use of this rule, we may apply it to the harmonic constants in table 3 for Key West, Cedar Keys, Galveston, and Habana. From table 3, the values of $M_2°-(K_1°+O_1°)$ are, disregarding the sign of the result: Key West, 641°, or after subtracting from $2 \times 360°$ gives 79°; Cedar Keys, 122°; Galveston 152°; Habana 32°. In accordance with the above rule, Key West with a value of 79° should exhibit inequality in both the high and low waters with the high water inequality somewhat the higher; Cedar Keys, with 122° should likewise exhibit inequality in both the high and low waters but with the greater inequality in the low waters; Galveston, with 152° should exhibit the inequality principally in the low waters; Habana, with 21° should have its inequality principally in the high waters. Looking back to figures 23, 24, and 26, it is found that the tide curves at these places conform to the findings from the harmonic constants.

In the discussion of the different types of tide, spring tides were defined as those coming "near the times of new and full moon" and tropic tides were defined as those coming "when the moon is near its maximum semimonthly declination." This somewhat indefinite phraseology is necessary because between any astronomical occurrence and the resulting maximum effect upon the tide there is usually a lag. In the spring or neap tides this lag is known as the phase age, and for the tropic or equatorial tides it is known as the diurnal age. These ages vary from place to place but can very readily be computed from the harmonic constants. In hours, the phase age is given by the formula 0.98 $(S_2°-M_2°)$ and the diurnal age by 0.91 $(K_1°-O_1°)$. Thus, from table 3 we find that at Key West, spring tides come 0.98 $(101-77)=23.5$ hours, or a day after full or new moon; and at Pensacola, tropic tides come 0.91 $(56-47)=8$ hours, or a third of a day after the moon's maximum semimonthly declination.

The harmonic constants lend themselves to the derivation of various other features of the tides, but the necessary formulae and calculations are rather involved and would be out of place here. The interested reader is referred to U. S. Coast and Geodetic Survey Sp. Pub. 260, Manual of Harmonic Constant Reductions.

DISTURBING EFFECTS OF WIND AND WEATHER

The regularity in the periodic rise and fall of the tide and in its cyclic variation is subject to the disturbing effects of changing meteorological conditions. These disturbances arise primarily

from the changes in the level of the water brought about by the changing meteorological conditions. In changing the level of the water from which the tide rises and falls wind and weather disturb both the times of occurrence and the heights of the high and low waters.

With respect to the disturbances brought about by changes in barometric pressure the water in any coastal body of water may be regarded as constituting a huge water barometer. When the barometric pressure over this body of water rises as compared with the pressure over the open sea the water inside will fall, while with a lesser pressure the water will rise. Since the specific gravity of mercury is about 13 times that of water a change in barometric pressure of 1 inch should be accompanied by a change in the level of the water of a little more than a foot.

Actually, however, the matter is not quite so simple, for it is not so much a question of difference in barometric pressure over a coastal body of water and the open sea as it is of barometric gradient. Furthermore, pressure differences are accompanied by winds, and the effects of the latter on the rise and fall of the tide are much more pronounced than the direct effects of barometric pressure.

From general considerations, it is clear that in waters having equal ranges of tide the same wind will have greater disturbing effects in the body of water having the lesser depth. Likewise, in bodies of water of equal depth, a given wind will be accompanied by greater disturbing effects in the body of water having the lesser range. Finally, in waters having equal depths and ranges of tide, wind effects are more disturbing on tides of the mixed and daily types than on tides of the semidaily type, and since in the Gulf the depths are relatively shallow, the ranges of tide rather small and the type of tide mixed and diurnal, it is to be expected that the disturbing effect of the wind on the tide will be quite pronounced.

For any particular stretch of coast, too, the hydrographic features enter as factors into the effects of a given wind. The problem is therefore a complex one necessitating detailed studies for each body of water. Such studies are almost completely wanting. In connection with notable storms, the heights attained by high water will be noted by the meteorologist or engineer studying the effects of the storm in a particular harbor.[1]

Needed, too, are studies correlating to the height of the tide at various places to storm tracks so that approximately accurate predictions of the height of a storm tide to be expected may be made from the characteristics of a developing meteorological disturbance. A closely related problem, the use of observed changes in the tide to furnish information regarding the direction and movement of a storm still far out in the Gulf, is discussed by Cline (1920).

In bays and harbors receiving the flow from large drainage areas the tides are also subject to disturbances arising from variations in run-off. In general, however, these disturbing effects become pronounced only in the upper reaches of tidal streams.

THE TIDE IN THE GULF OF MEXICO

Thus far, the discussion of the tides at various places in the Gulf of Mexico has considered the tide at each place as a local phenomenon. How do these tides tie together? In other words, what is the dynamics of the tidal movement in the Gulf as a whole? What explains the relatively large diurnal component in the Gulf as compared with the Atlantic Ocean? Only few investigations of this character have appeared in print.

S. F. Grace (1932) briefly reviews the explanations offered by various investigators. The dynamics of the tide in any large body of water is a difficult problem. In the Gulf of Mexico, it is further complicated by the irregular shape of the basin and by its connections with the Atlantic Ocean and the Caribbean Sea which pose the question of co-oscillation with the tidal movements in those bodies of water.

Qualitatively, the simplest explanation of the relatively large diurnal component in the Gulf is that the length and depth of its basin are such that its free period of oscillation approximates 24 hours; that is, it approximates the period of the diurnal tide-producing forces and therefore responds better to the diurnal forces than to the semidiurnal forces.

[1] See for example: The Galveston Hurricane of September 8, 1900, Monthly Weather Review, Sept. 1900, pp. 371–377, and The Tidal Storm at Corpus Christi and Its Effect on Engineering Structures, Engineering News-Record, Nov. 13–20, 1919, pp. 848–852.

In the above-mentioned article, Grace studied the K_1 component and constructed a cotidal chart for that component from which "the motion appears to be that of a wave entering through Florida Channel, progressing round the basin in the positive sense, suffering reflexion at the northwesterly and southerly coasts, and leaving by Yucatan Channel; the time occupied by this progression is about six hours."

SEA LEVEL

The term "sea level" is used to designate the level or elevation of the sea from which the tide rises and falls. In other words, it is the level of the sea freed from the rise and fall of the tide and is derived by averaging the hourly heights of the tide for a period of one or more days. It is convenient, too, to use the expressions daily sea level, monthly sea level, and yearly sea level to denote, respectively, the sea level derived by averaging the hourly heights of the tide for the period of a day, month, or year.

If the hourly heights of the tide at any place are averaged for each day over a number of days, it is found that sea level fluctuates from day to day by amounts varying from less than a tenth of a foot to more than a foot. During a single month sea level on one day may differ by several feet from that on another day. These relatively large fluctuations are obviously to be ascribed to the effects of wind and weather which vary from day to day.

If now we derive sea level for a month, we find that from one month to another sea level may fluctuate by as much as half a foot, and within a year, two monthly values of sea level may differ by a foot. Since the seasonal change in wind and weather is largely periodic, the question arises whether the change in monthly sea level likewise is periodic. On investigation, this is found to be the case, and in figure 32 are shown the average heights of monthly sea level at nine tide stations in the Gulf of Mexico based on three or more years of observations.

It is customary to explain the annual variation in sea level as due primarily to the effects of wind and weather, but studies giving quantitative relationships in the Gulf of Mexico between the annual variation in sea level on the one hand and wind and weather on the other hand are wanting. In general, it is seen that throughout the Gulf sea level is low in the first half of the year and high in the autumn. It is of interest to note, too, on the United States coast, the marked increase in the secondary minimum in the summer at the stations west of the Mississippi River.

The curves of annual variation for Coatzacoalcos, Progreso, and Habana must be considered as approximate only, being based on a few years of observations.

In connection with the determination of mean sea level at any place, it is clear that in view of the seasonal variation in sea level, a month of observations can give only an approximate value. Within a year, however, the seasonal variation is eliminated, and the fluctuations due to the disturbing effects of wind and weather tend to balance out. In figure 33 are shown the yearly values of sea level at the four stations for which 20 years or more of observations are available.

Disregarding for the moment the dashed-line curve associated with each of the diagrams, it is seen that sea level from one year to another may differ by amounts varying from several hundredths of a foot to several tenths of a foot. The larger fluctuations must obviously be ascribed to the disturbing effects of wind and weather which do not repeat themselves exactly from year to year. These fluctuations can be eliminated by smoothing by moving means, and a more or less smooth curve derived. In that manner, the dashed-line curve for each of the yearly sea level diagrams was derived.

For Key West, there appears to have been little change in sea level from 1913 to 1930, after which there appears to be a more or less regular rise amounting to 0.37 foot by 1950, or a little less than 0.02 foot per year. In this connection, it is of interest to note that the change in sea level at this station approximates the change found at the tide stations along the Atlantic coast of the United States from Florida to Massachusetts (Marmer 1949).

At Cedar Keys the break in the observations from 1925 to 1938 allows only tentative conclusions, but the evidence is for little change in sea level between 1915 and 1925 and a gradual rise from 1939 to 1950 of about 0.3 foot. This gives a rise at the rate of a little over 0.02 foot per year

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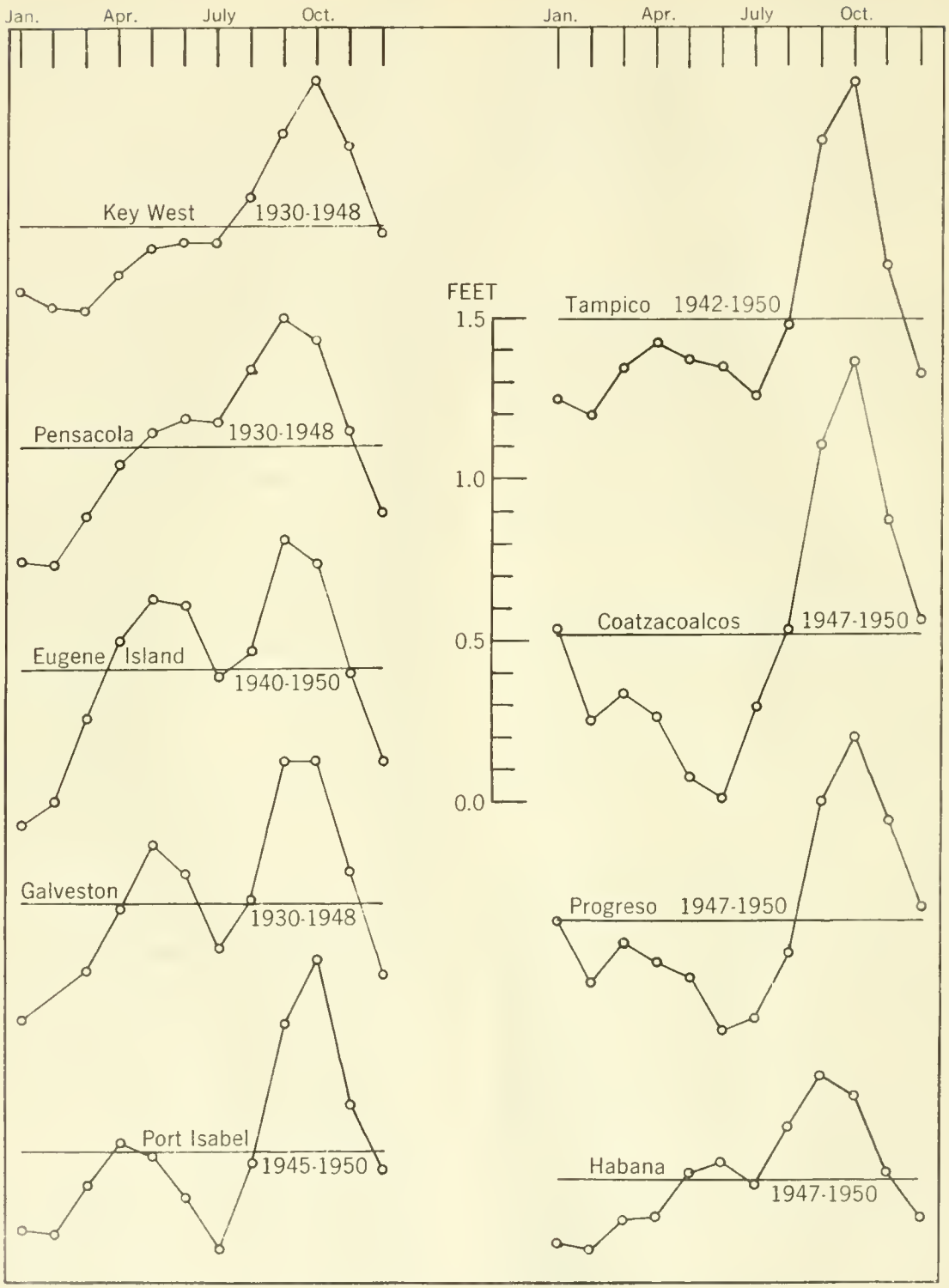

FIGURE 32.—Annual variation in sea level at nine tide stations, Gulf of Mexico.

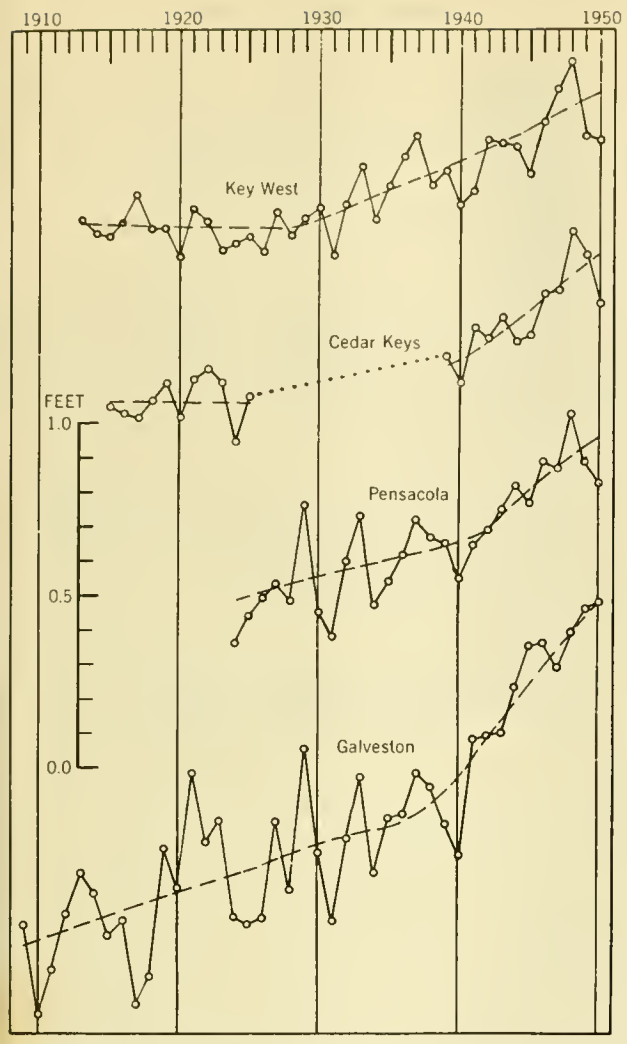

FIGURE 33.—Yearly sea level, Key West, Cedar Keys, Pensacola, and Galveston.

for the past 11 years, or at a rate somewhat larger than at Key West.

At Pensacola, the rise in sea level from 1924 to 1950 is very nearly half a foot. From 1924 to 1941 the rise was at the rate of about 0.01 foot per year, but since then the rate appears to be a little over 0.03 foot per year.

At Galveston, the change in sea level from 1909 to 1950 is almost exactly 1 foot. From the diagram of figure 33, sea level appears to have risen more or less uniformly from 1909 to 1937 about 0.4 foot or at the rate of 0.014 foot per year. From 1938 to 1950 sea level rose 0.6 foot or at the rate of 0.05 foot per year or at a rate more than three times that of the earlier period.

For the northern shores of the Gulf the observations available indicate a rise of sea level in recent years but at different rates at the different places. Furthermore, in the last decade or two the rise has been at a more rapid rate at all four stations of figure 33. These matters clearly pose questions of a geophysical nature which fall outside the restricted field of tides.

It is of interest to note, however, that a change of sea level at a given place may be due to one or more of several different causes. Clearly, if a coastal area is subsiding, sea level in that area will rise relative to the coast, but a rise in sea level will also occur along a stable coast if the volume of the water in the open sea has increased. It appears likely that such an increase, at a very slow rate to be sure, is taking place at the present time through an amelioration of the climate in high latitudes, testified to by the recession of glaciers, the melting waters of which are finding their way to the open sea. Long-continued deposition in the sea of river-borne material from the land tends to decrease the depths of the sea and thus cause a rise of sea level. Finally, even with stability of the coast, of the volume of water in the sea, and of the depths of the sea, a rise in sea level at a particular place may conceivably occur through a change in the seasonal distribution of the direction and velocity of the winds.

AVAILABILITY OF TIDAL DATA

Tidal data for the Gulf of Mexico are available in various forms. Tide Tables, East Coast, North and South America, issued annually in advance, give daily predictions for a calendar year of the heights and times of high and low water for Key West, Tampa Bay, St. Mark's River entrance, Pensacola, Mobile, Galveston, and Tampico Harbor. In addition, these tables list Tidal Differences and Constants for many other places in the Gulf which permit approximate predictions to be made by reference to the above standard stations.

The Coast and Geodetic Survey also issues, in looseleaf form, descriptions and elevations of the tidal bench marks it has established in various places along the United States coast of the Gulf. These describe the location of each bench mark and its elevation above mean low water. For each

locality there is given, in addition, a table listing the highest and lowest tides observed or inferred, and the heights of mean high water, half tide level, and mean low water.

At the present time, there are in operation by the Coast and Geodetic Survey 10 primary tide stations located as follows: in Florida, at Key West, St. Petersburg, Cedar Keys, and Pensacola; in Louisiana, at New Orleans, Bayou Rigaud, and Eugene Island; in Texas, at Galveston, Rockport, and Port Isabel. Most of these stations have been in operation for a number of years, at Galveston, for example, since 1909. For each of these stations there are available, in the files of the Coast and Geodetic Survey at Washington, tabulations giving the hourly heights of the tide and the times and heights of high and low waters. There are also available summaries giving the monthly and yearly heights of high water, low water, and sea level.

Tide stations have also been operated in recent years by the governments of Mexico and Cuba.

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PHYSICAL OCEANOGRAPHY OF THE GULF OF MEXICO [1]

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Oceanography may be defined as the study of the oceans in all their aspects, including the interrelationships between the seas and their boundaries—the atmosphere, the shoreline, and the sea bottom. Physical oceanography consists of the analysis of the physical properties of sea water, the study of motions in the oceans such as those associated with ocean waves, tides, and winds, and examinations of the various mechanisms for the transfer and interchange of energy.

The nature of physical oceanography differs from that of the other aspects of the subject in that certain investigations may be conducted somewhat independently. The other generally recognized aspects of oceanography are the biological, the chemical, the geological, and the meteorological. Investigations in these are usually dependent upon physical oceanography and upon each other. It is desirable that work in the physical aspect be planned jointly with that in the other aspects in order that maximum utilization may be made of results which are obtained. The physical oceanographer must pay particular attention to the problems in the other branches of the work since one of the primary objectives of his own researches is the development of information needed for the solution of some of these problems.

There are many unique opportunities in the study of physical oceanography in the Gulf of Mexico. There is an offshore oil industry facing many problems related to construction and operation in the shallow waters over the wide continental shelf, there is a huge chemical industry which has an output depending heavily upon the varying longshore currents which alter the salt content of the water at the position where it is taken into the plants, and there are many characteristic weather features such as hurricanes, squalls, and fog which result from effects of the oceans upon the atmosphere. Further, the large oyster and shrimp fisheries are markedly affected by currents, turbulence and the physical characteristics of the sea water. Also, in reduction of beach contamination, prevention of beach erosion, reduction of dredging costs in marine channels, increasing the efficiency of marine transportation, development of recreational areas on the beaches, and in providing oceanographic information critical to the defense of our coastline, physical oceanography plays a most important role in the Gulf of Mexico.

The Gulf, being nearly enclosed, provides a model ocean in which much may be learned about processes operating in the larger oceans which are not so readily adaptable to comprehensive and systematic analysis. The presence of fixed platforms far from shore may make it possible for the first time to make such determinations as that of the effect of the wind in changing the slope of the sea surface in the open sea. Such information is needed for further development of the theories of wind stress upon the sea surface and for the more complete understanding of the manner in which the winds drive the ocean currents and set up ocean waves.

Despite the need for physical information in the Gulf, relatively little has as yet been done to survey the region systematically and to provide information in a form which is generally available. Recently there have been increased efforts in this direction, and within the near future it may be expected that knowledge of this highly important oceanic region will be greatly increased.

OCEAN CURRENTS

The primary problem in the physical oceanography of any region is the determination of the ocean currents. In the Gulf of Mexico it is particularly difficult. To provide a background for a discussion of this problem it is well to consider

[1] Contribution from the Department of Oceanography of the Agricultural and Mechanical College of Texas, Oceanographic Series No. 16; based in part on investigations conducted for the Texas A. and M. Research Foundation, through the sponsorship of the U. S. Navy Office of Naval Research.

briefly the general nature of the currents which may be expected in such a region.

The general nature of currents in the Gulf of Mexico

Sverdrup (1942) [2] lists three different groups of currents each of which is represented in the Gulf of Mexico. These are:

(1) currents that are related to the distribution of density in the sea,

(2) currents that are caused directly by the stress that the wind exerts on the sea surface, and

(3) tidal currents and currents associated with internal waves.

Tidal currents [3] are caused by the tide-producing forces. These forces result from differences between the constant centrifugal force which acts on any particle on the earth and the varying gravitational attractions between the earth, the moon, and the sun. These attractions are proportional to the masses of the bodies and inversely proportional to the squares of the distances between them. Because of its very short distance from the earth the attraction of the moon is large. The sun, on the other hand, although it is at a much greater distance from the earth, is so large that a tide-producing force results which is as much as 46 percent of that of the moon.

The direct result of tide-producing forces acting upon the rotating earth is to raise and lower periodically the level of the ocean's surface, i. e., to create tides. Water which is required to raise sea level at a particular location must be furnished by horizontal movements within the ocean. These are the tidal currents. Since the sun and moon change their position with respect to a given part of the earth's surface in a periodic fashion, the tides and tidal currents are periodic. Because the rotation of the earth affects movements of water the tidal currents do not oscillate back and forth on a straight line but rotate. In the Northern Hemisphere this rotation usually is in a clockwise direction except where modified by other factors. At times, interference between tidal waves or the influence of other forces is such that the rotation may be counterclockwise.

Along the Gulf coast there are many bays and lagoons which have relatively restricted outlets to the sea. If the water level in these bays is to be raised by tidal action, all of the water required for the change in level must flow into the bay through these restricted channels. Therefore, the tidal currents in such channels may be quite large, particularly at certain stages of the tide.

The great width of the shallow continental shelf along the Gulf coast results in tidal current velocities which are relatively high considering the small range of tide. This is because the change of water level of this large area over the shelf must be brought about by flow across the shallow shelf. Since the depth of the moving water is small, its velocity must be relatively great to provide the volume needed for change in sea level. The high velocities and the changing direction and speed of these tidal currents may lead to considerable turbulence and stirring in certain localities.

Oscillating currents related to internal waves may be important in this region, but little information now is available on this subject.

Currents caused by the stress of the wind upon the sea surface are particularly important on the Gulf coast. The most widely known phenomenon which results from the action of such currents is the storm tide or general rise in water level which precedes winds of hurricane velocities. Storm tides are discussed by Cline (1920) and Tannehill (1927). Some of their results are summarized in the chapter on meteorological phenomena.

When a wind starts to blow over the ocean it exerts a frictional force or drag upon the sea surface. If the wind persists the surface layers of the water start to move and they in turn act upon the deeper layers and set these in motion also. The two forces which are involved in setting up such currents are the frictional force, and the Coriolis force which is the apparent force due to the rotation of the earth. If the wind blows long enough for a state of equilibrium to be reached, the surface waters away from the influence of the coast will be moving in a direction approximately 45° to the right of the wind direction in the Northern Hemisphere. A north wind sets up a surface current toward the southwest. The surface velocities may reach 1 to 2 percent of the wind velocity. Currents at greater depths will flow at greater angles to the wind and at speeds which decrease with depth.

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[2] References are listed at the end of the chapter.

[3] Tides in the Gulf of Mexico are discussed separately in the article by H. A. Marmer, pp. 101–118.

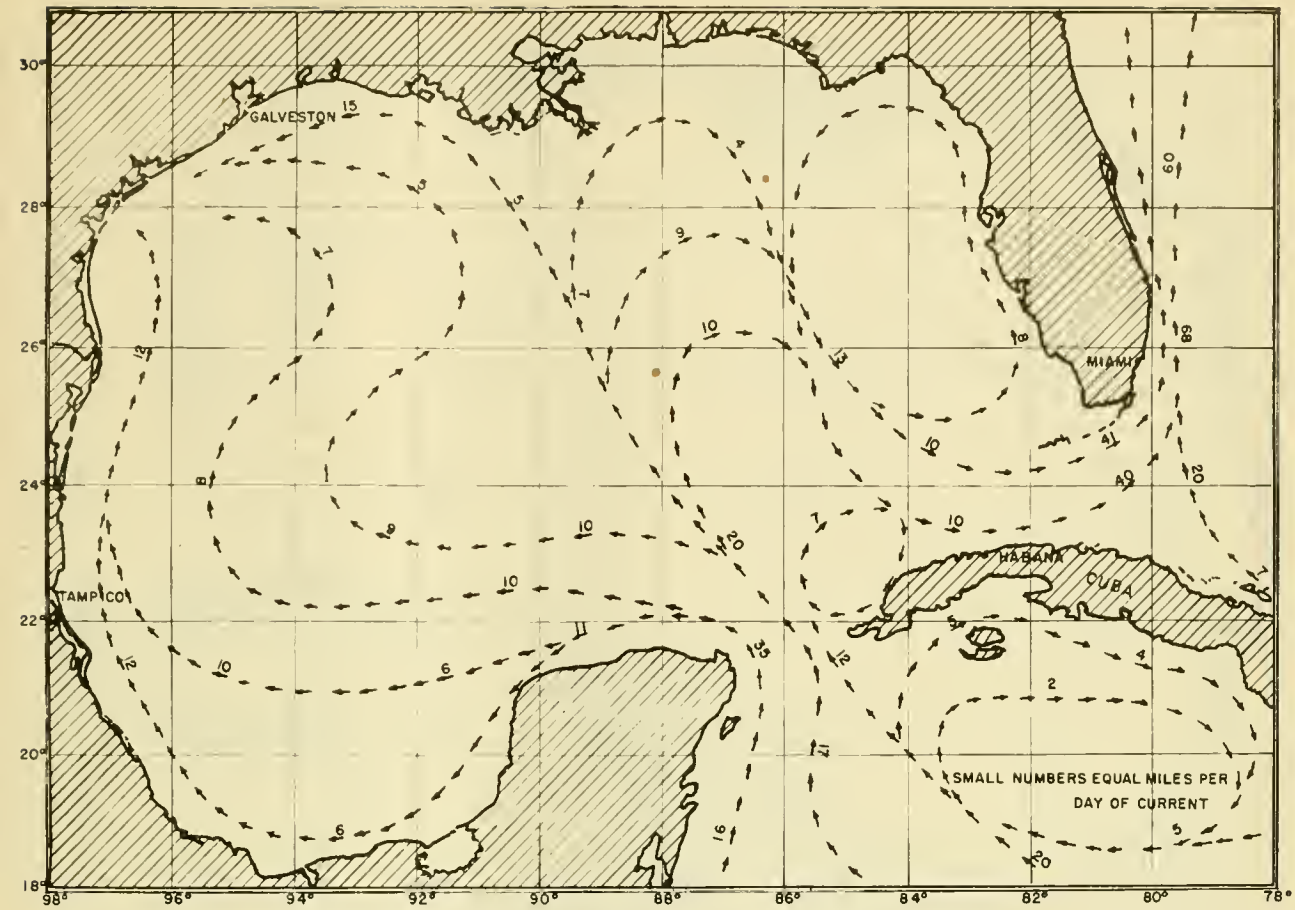

FIGURE 34.—Surface ocean currents in the Gulf of Mexico in June.

Conclusions concerning currents set up by the wind are mostly based upon theoretical considerations. A few observations have been made in landlocked bays to show the piling up of water by the wind. However, in the open ocean no systematic data are available. The drilling platforms off the Gulf coast permit the accumulation of data which will make possible a practical analysis.

The currents related to the distribution of density are the major semipermanent currents of the oceans. Little is known about these currents in the Gulf of Mexico. The chief source of information is the pilot charts of the United States Navy Hydrographic Office (figs. 34 and 35). These are based upon the navigation records of the ships sailing in the Gulf over many years. They do indicate the general drift in various regions, but the individual observations upon which they are based are subject to many errors. For example, the deviation of a ship from its course may be caused by the wind rather than by the current. Also, it is difficult to determine positions at sea accurately. A survey of the pilot charts for the Gulf indicates that these may not describe all of the currents present. They show waters flowing into the western part of the area at all latitudes but no water flowing out. This situation cannot exist unless there is a submarine return current of equal magnitude, which seems unlikely.

In the deep waters, direct observation of current velocities has been almost impossible until recently because of difficulty in anchoring vessels. Accordingly, few such observations have been made. Instead, oceanographers have developed a method based upon principles of physics. By use of this method the ocean currents present may be inferred from the distribution of density as determined by relatively simple observations of temperature, salinity, and pressure. Two forces again

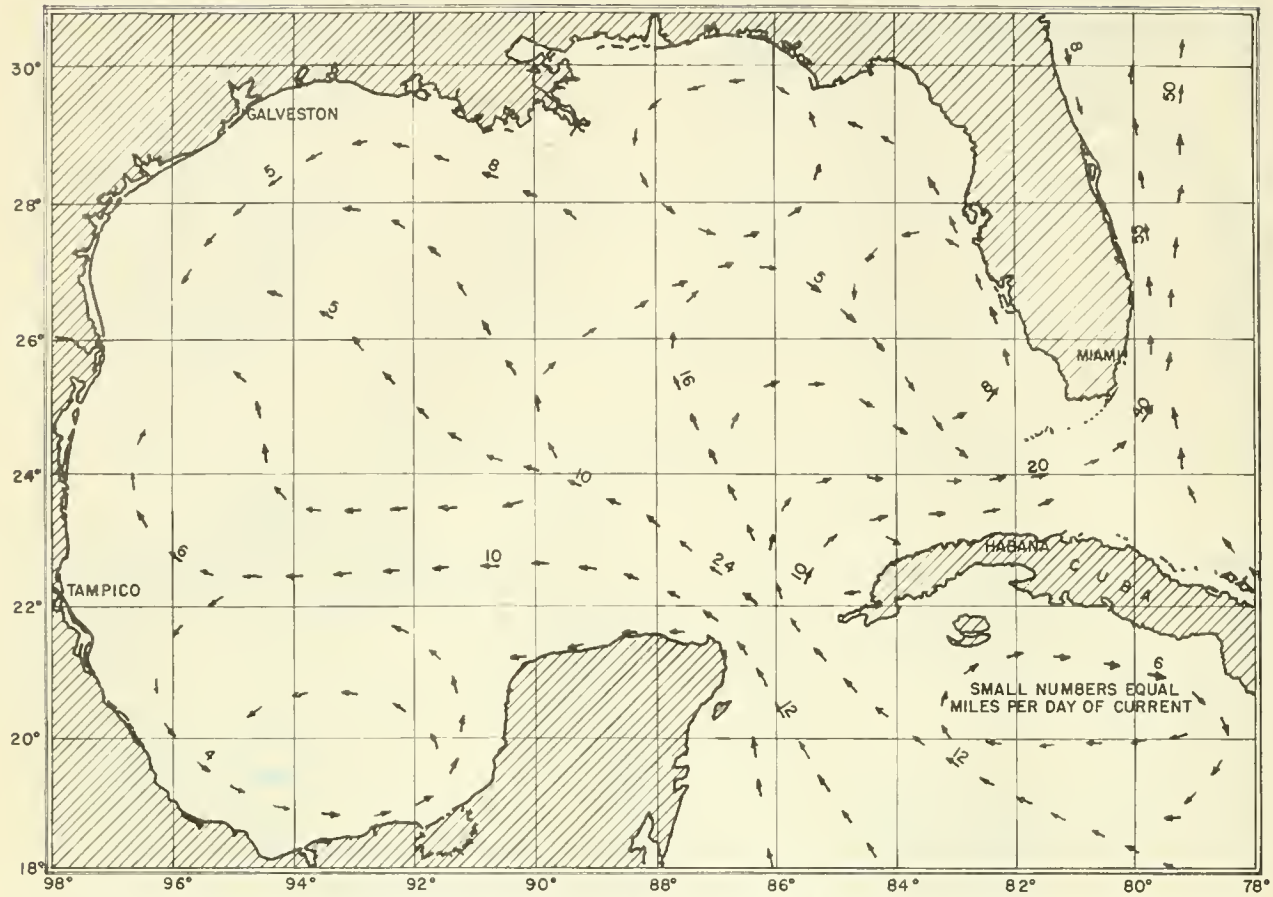

FIGURE 35.—Surface ocean currents in the Gulf of Mexico in December.

are involved, one of these being the Coriolis force and the other the "pressure force" which is a force that depends upon the water density distribution in the earth's gravitational field. The pressure force tends to make water flow from a region of high pressure toward a region of low pressure just as water poured into less dense oil will flow outward from the point at which it is poured. When the movement related to the pressure gradient has begun, the Coriolis force acts toward the right of the movement in the Northern Hemisphere and the resulting equilibrium between the two forces is associated with a steady current flowing almost perpendicular to a line connecting the regions of high pressure and low pressure. This flow is such that in the Northern Hemisphere the more dense water is on the left of a person standing with his back to the current and the less dense water is on his right. Since temperature is one of the major factors influencing density, it may be inferred that the cold water is on the observer's left and the warm is on his right when he is standing as described above with relation to the current. Thus, he can tell something about the currents if he knows the distribution of temperature, or he can tell something about the temperature if he knows the distribution of currents.

There are a number of difficulties which arise in applying the current computation method. These occur partly because the basic assumptions underlying the theory are not always fulfilled. However, despite these difficulties the method has been found to be the one which provides the most information for a reasonable amount of work. It is not known how accurately the Gulf currents in deep water may be determined by this method, but there is reason to believe it to be the most

accurate of the methods now in use. Used in conjunction with the geomagnetic electrokinetograph, it probably provides the best complete picture of the current patterns in the open Gulf. Determination of the flow over the broad, shallow continental shelf remains a difficult problem.

Some processes by which the distribution of density is caused to change are evaporation, conduction, and the movement of masses of water by the winds. Since the total transport of water due to the winds in this hemisphere is toward the right of the wind, and since this transport consists of waters in the surface layers which are warm and of low density, the low density waters are piled up at the right of the wind flow, which is in the center of anticyclones, regions of good clear weather. The warm waters are removed from the low pressure storm areas at the left by the wind action. These movements are called the wind-driven currents. Their primary effect is to pile up water of small density in areas of anticyclonic winds and to leave waters of greater density in areas of cyclonic winds. This leads to a secondary effect, namely, the maintenance of a different ocean current related to this distribution of density. Since such currents flow nearly perpendicular to a line connecting the regions having the different water densities, the associated currents form a pattern quite similar to the pattern of the winds. This may readily be recognized on charts showing the distribution of ocean currents with prevailing winds superimposed.

Investigations of ocean currents in the Gulf of Mexico

There is probably no part of the oceans of the world of comparable size to the Gulf of Mexico where there is such a wide difference of opinion concerning the specific current regime. This difference is brought out by Sweitzer (1898). He quotes Isaac Vassius who, writing about the year 1663, tells how the currents through the Yucatán Channel "turn obliquely" and pass through the Straits of Florida. The issue of the Encyclopedia Britannica available in 1898 states that "a portion of it (the current—DFL) passes directly to the northeast along the shore of Cuba; but by far the larger part sweeps around the Gulf." Sweitzer himself concludes that, at times "the channel of Yucatán pours its waters into the Gulf so that they spread out in all directions moving on its center," while at other times the currents flow "in a northeasterly direction around the extreme west coast of Cuba." These last results were based upon studies of the distribution of specific gravity of the surface waters, United States Coast and Geodetic Survey, Lindenkohl (1896), and upon modification of currents by the prevailing winds.

Sweitzer also reported considerable agitation of the waters covering an area of about 100 square miles occurring off the coast of Texas about 40 miles south and 20 miles east of Aransas Pass which could only be accounted for by the meeting of two opposing currents. Other evidence of converging currents has since been found, and this area has become known as the graveyard of ships.

Measurements made in the years 1885 to 1889 by the United States Coast and Geodetic Survey vessel *Blake*, commanded by Pillsbury (1889), determined the currents in the Straits of Florida. Since the ship was anchored, direct current observations could be compared to computed values, and the comparison provided one of the best examples illustrating the validity of the method for computing relative currents which is now so widely used.

Agassiz (1888) published temperature and salinity data collected by the *Blake* in 1878. These data, together with others collected by the *Bache*, Bigelow (1917), were used by Wüst to compute the transport of the water through the Florida Straits as 26 million m^3/second. Associated with this transport is a water level difference of 19 cm. between the southeastern Gulf and the Atlantic at St. Augustine, Florida, which is discussed by Montgomery (1938). A theory of piling up water in the "Bay of Mexico" was advocated by Benjamin Franklin about 1770.

In 1922, the *Dana* made some observations in the Yucatán Channel and in the Florida Straits, as shown in figure 36. These observations, as well as those of the *Mabel Taylor* in 1932, were summarized by Parr (1935) who concluded that "evidence thus obtained from the Gulf itself, although directly opposed to some of his premises, nevertheless serves to confirm the theory already advanced by Nielsen on the basis of observations in the Straits alone, that the so-called Gulf Stream only takes the shortest possible path from its entrance through the Yucatán Channel to its

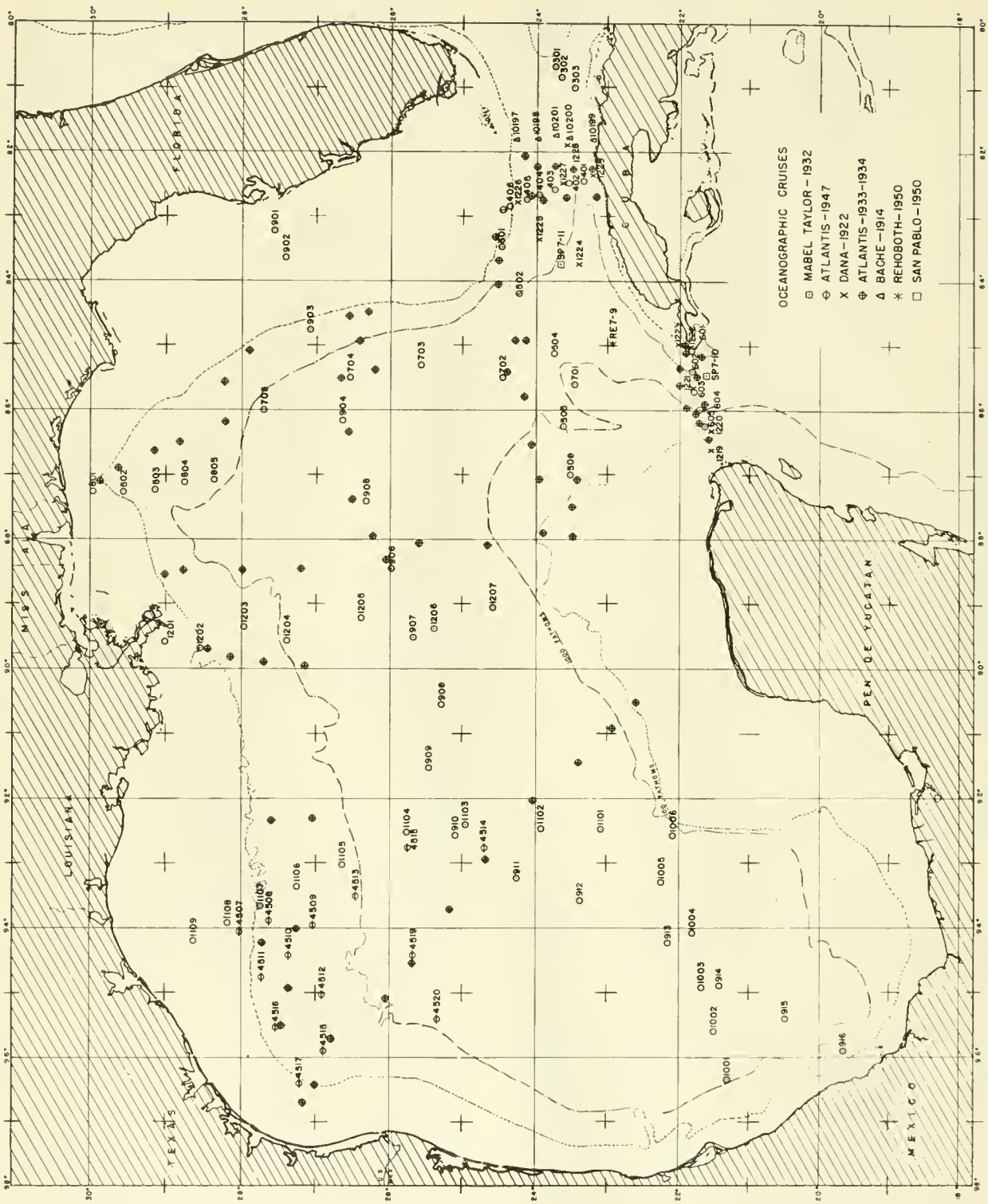

FIGURE 36.—Hydrographic stations in Gulf of Mexico.

exit through the Straits of Florida, without deviating on the way, or diffusing any to itself significant amount into the Gulf of Mexico proper, or receiving any predominant contribution from the Gulf in return." This statement on the one hand and the current pattern shown in figures 34 and 35 on the other hand summarize the present divergence of opinion.

The *Mabel Taylor* cruise was made without unprotected thermometers or other reliable means of determining depth of observations. Parr cautions that particularly in the Yucatán Channel and Florida Straits there is sufficient uncertainty of the depths of the *Mabel Taylor* operations "to make it seem inadvisable to subject them to a form of analysis and comparison in which depth is an essential consideration." Similarly, the *Atlantis* cruise of 1934, Parr (1937), lacks subsurface data since the hydrographic cable was lost early in the survey. Thus, the oceanographic data available to Parr were meager.

Dietrich (1939) reviewed the currents of the Gulf, and his conclusions, although based upon essentially the same data as used by Parr, show considerably more influence by the Gulf Stream upon the general circulation in the Gulf. He discussed the sill depths showing that the Gulf circulation cannot affect the deep water circulation of the Atlantic below about 800 meters. However, the Florida current, which is shallower than this, has considerable effect.

In 1947 the *Atlantis* conducted a survey of the northwestern Gulf making 27 hydrographic stations (fig. 36) and 473 bathythermograph observations of temperature. These data have been analyzed by Fred B. Phleger (1951), now of the Scripps Institution of Oceanography of the University of California, and have been published by the Geological Society of America.

The first cruises of the *Alaska*, oceanographic research vessel of the Fish and Wildlife Service operating on a survey of the Gulf of Mexico with the cooperation of the Department of Oceanography of Texas Agricultural and Mechanical College and the United States Navy, Office of Naval Research, were completed in October 1951 (fig. 37). These provide the first complete coverage of the Gulf with information needed to compute the deep water currents. The data from these cruises have been distributed and prelimary analyses indicate that they support the main features of the current pattern shown in figure 34.

A brief description of the currents of the Gulf of Mexico is provided in the United States Coast Pilot (1949):

> Under normal conditions, at all seasons of the year, the great volume of water passing northward through Yucatán Channel into the Gulf of Mexico, spreads out in various directions. Surface flows set westward across Campeche Bank, the Gulf of Campeche, and the Sigsbee Deep; northwestward toward Galveston and Port Arthur; north-northwestward toward the Mississippi Passes; and eastward into the Straits of Florida.
>
> A straight line drawn from Buenavista Key, Western Cuba, to the Mississippi Passes forms an approximate boundary between movements having different directions. West of this line the drift is generally northward or westward, while east of it the drift is eastward or southeastward toward the Straits of Florida.
>
> There are northward flows along the west side of the Gulf between Tampico and Corpus Christi in the vicinity of the 100-fathom and 1,000-fathom curves, north of the Sigsbee Deep between the 2,000-fathom and the 100-fathom curves, and along the west coast of Florida.
>
> In general, the surface circulation is the same at all seasons. There is, however, some seasonal change in velocity, the flow being generally stronger in spring and summer than in the autumn and winter.
>
> The current near the Florida Keys is variable and uncertain.

This description is apparently taken from the Pilot Chart series of the Hydrographic Office (H. O. No. 3500, issued monthly). Another series, H. O. No. 10,690, 1 to 12, Current Charts of the Central American Waters, give resultant direction and velocity for each 1° quadrangle of latitude and longitude. This series has been used by Smith, et al. (1951), to show zones where seasonal convergence or divergence occur.

Many of the references cited above contain bibliographies pertinent to the Gulf of Mexico. Also, Geyer (1950) lists many useful works.

In summary, the currents of the Gulf of Mexico and their variations are not specifically known. Studies completed in the past indicate some unusual and interesting features and provide incentive and justification for continued intensive investigation.

SEA SURFACE TEMPERATURES

A large number of sea surface temperature observations have been collected at shore stations. Some of these data from locations shown in figure

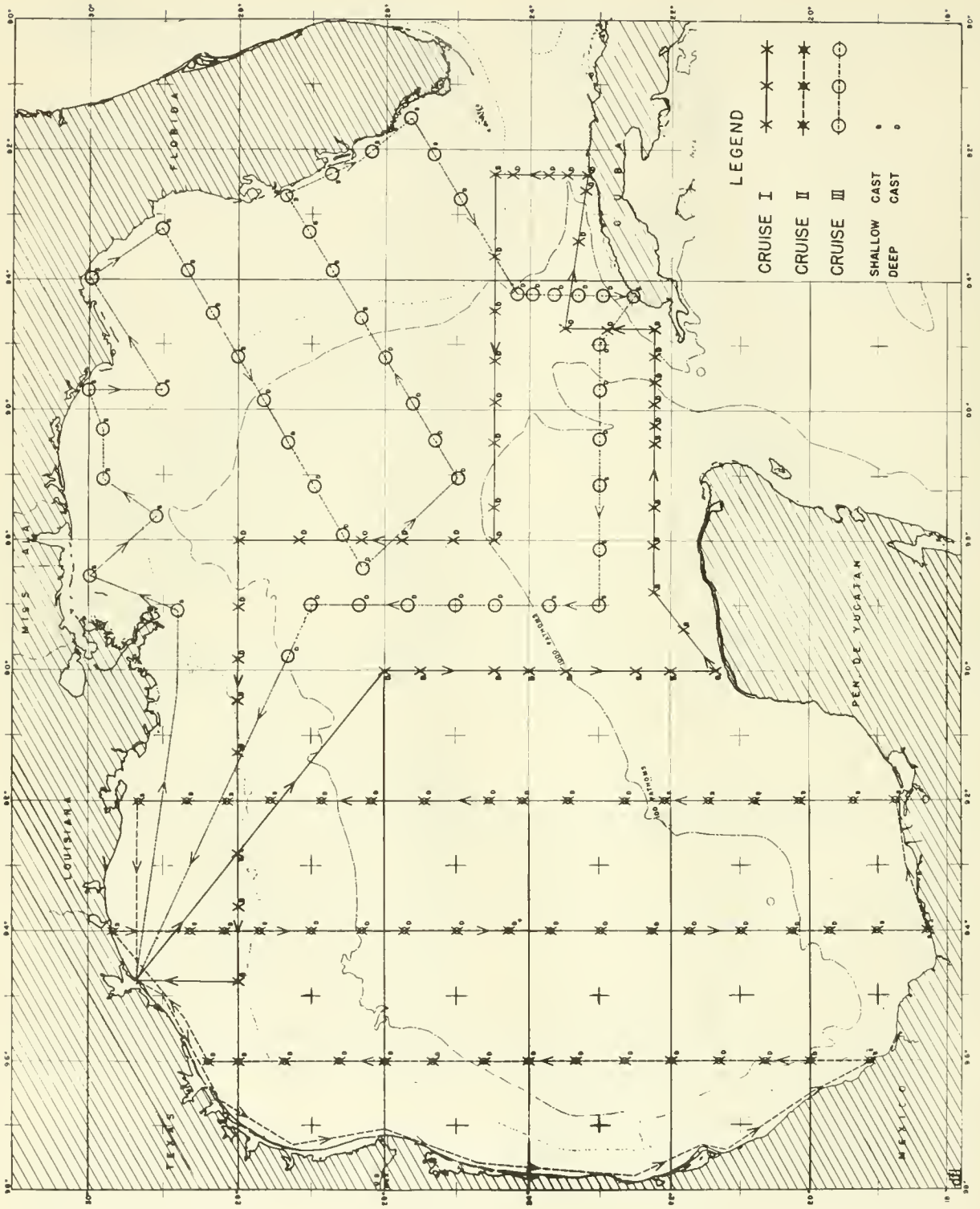

FIGURE 37.—Cruise plan for U. S. Fish and Wildlife vessel *Alaska*, September 1950.

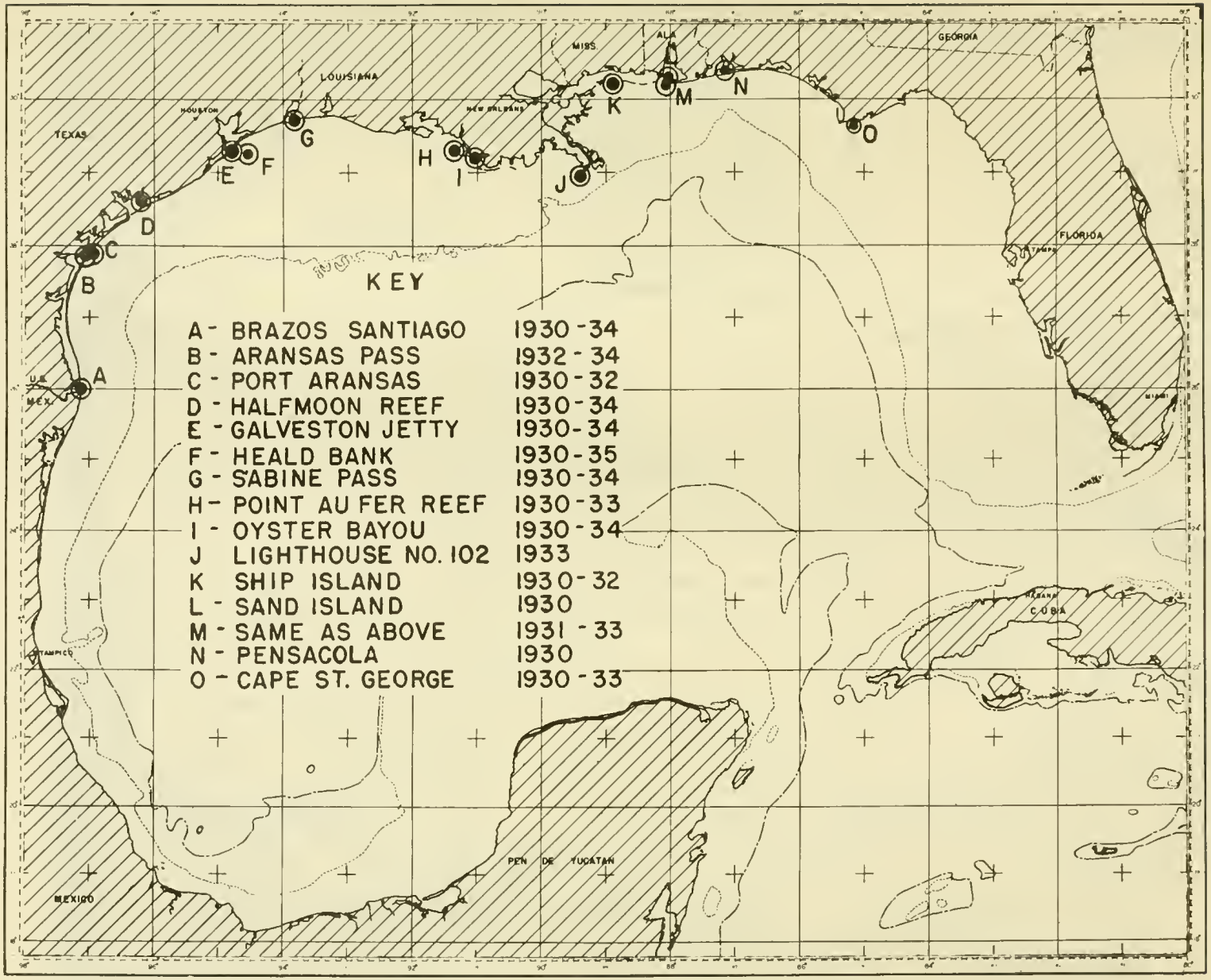

FIGURE 38.—Shore stations measuring sea surface temperature.

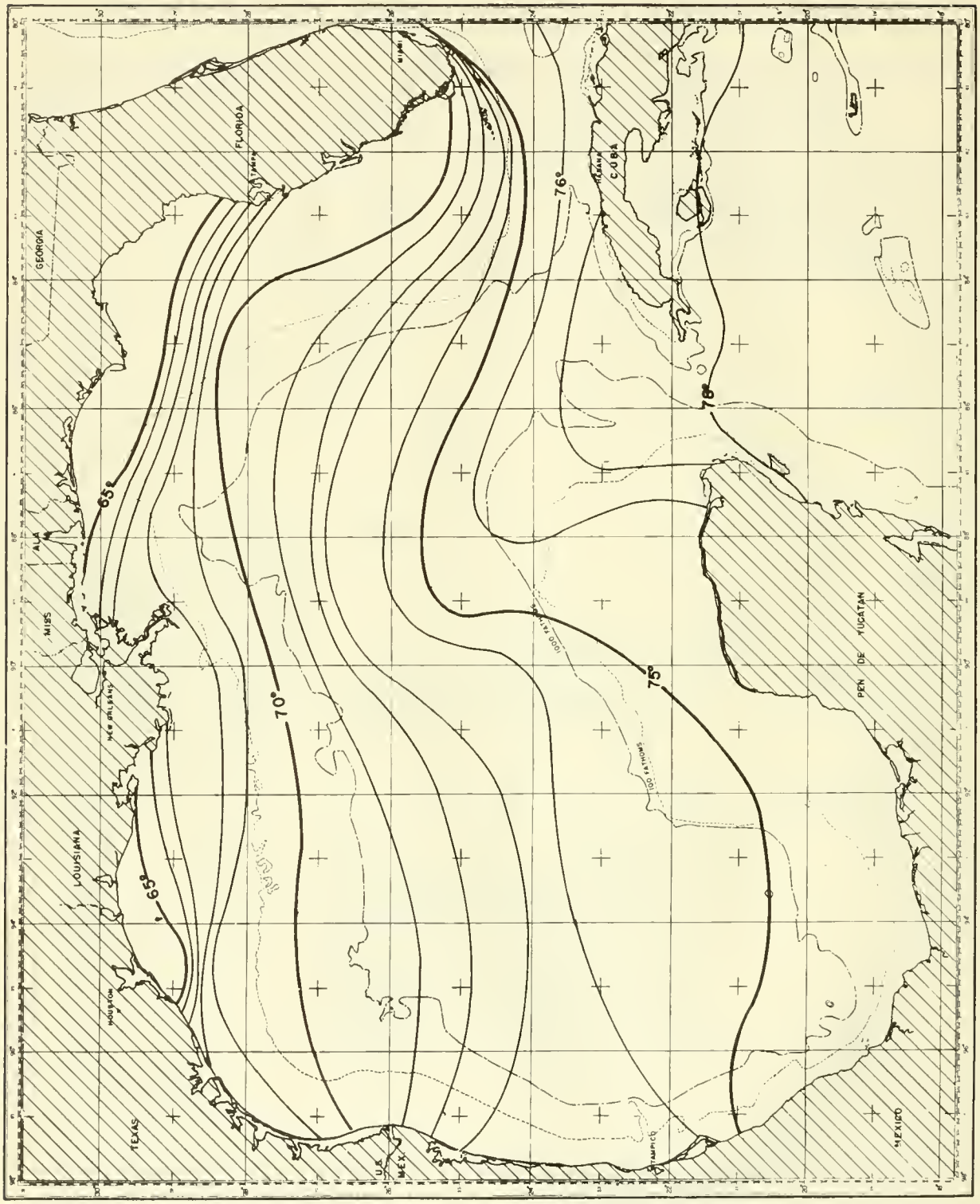

FIGURE 39.—Average sea surface temperatures for February (after Fuglister).

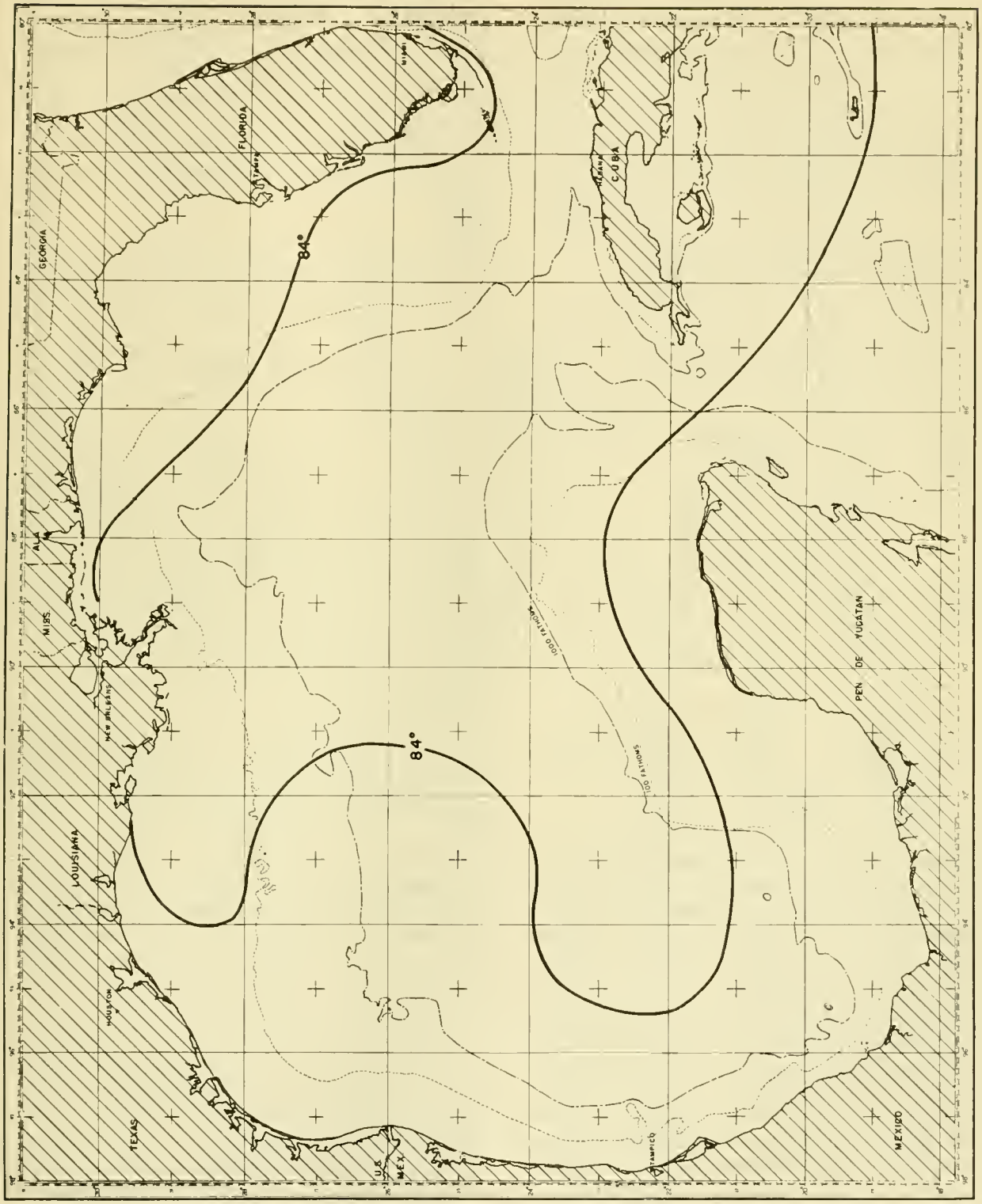

FIGURE 40.—Average sea surface temperatures for August (after Fuglister).

38 have been made available through the Fish and Wildlife Service of the United States Department of the Interior and are on file in the Department of Oceanography at Texas Agricultural and Mechanical College where a file-report has been prepared. The key in figure 38 shows the period of years in which observations were made and sent in from each station. The study of these shore station data is continuing, and references to additional information of this kind are sought. It is hoped that they may provide a clue to general changes which are occurring offshore where observations are not so readily obtainable.

Studies of sea surface temperatures in the Gulf of Mexico have been based on some 200,000 observations taken on ships in this area over a period of more than 50 years. The majority of these observations were made with the instruments carried as a regular part of each ship's equipment. Due to the possibility of error in the individual thermometers and to errors in reading, the results must be interpreted with care. However, with such a large number of observations the nonsystematic errors tend to cancel each other, with resulting averages being not far from the true mean.

The Weather Bureau of the United States Department of Commerce has computed average sea surface temperatures in the Gulf of Mexico using the above observations. Table 1 shows the aver-

TABLE 1.—*Monthly average sea surface and air temperatures in the Gulf of Mexico (in degrees Fahrenheit)*

[Figures in italics are averages of dry bulb thermometer readings observed as a rule on the ship's bridge. Figures in roman are mean sea surface temperatures, obtained mainly from bucket sampling]

Area	100–95W 30–25N		95–90W 30–25N		90–85W 30–25N		85–80W 30–25N		100–95W 25–20N		95–90W 25–20N		90–85W 25–20N		85–80W 25–20N	
Jannary	*66.8*	67.7	*63.6*	67.9	*68.1*	72.5	*69.3*	73.2	*70.7*	73.0	*72.5*	74.3	*74.1*	76.3	*71.9*	75.0
February	*66.9*	68.3	*63.7*	67.3	*68.3*	72.1	*69.2*	72.7	*70.4*	72.6	*72.7*	73.9	*74.1*	76.0	*72.1*	74.7
March	*67.5*	68.8	*66.3*	68.5	*69.8*	72.6	*70.9*	73.2	*72.7*	73.3	*73.9*	74.6	*75.3*	76.4	*73.3*	75.3
April	*73.3*	72.6	*71.1*	71.6	*73.3*	74.6	*74.0*	75.2	*75.4*	75.4	*76.2*	76.1	*77.1*	77.7	*75.9*	76.8
May	*75.6*	76.3	*75.9*	76.0	*77.3*	77.7	*77.5*	77.9	*78.6*	78.5	*78.8*	78.6	*79.4*	79.5	*78.7*	79.0
Jnne	*80.3*	80.5	*80.3*	80.6	*80.8*	81.0	*80.6*	80.8	*80.8*	81.1	*81.0*	81.2	*81.2*	81.6	*81.3*	81.5
July	*83.1*	82.6	*82.5*	83.1	*82.4*	82.9	*82.3*	82.6	*81.7*	82.5	*82.1*	82.4	*82.2*	82.6	*82.7*	83.0
August	*82.9*	83.3	*83.0*	83.9	*82.9*	83.7	*82.6*	83.4	*82.5*	83.3	*82.4*	83.2	*82.5*	83.2	*83.0*	83.8
September	*81.8*	83.3	*81.5*	82.8	*81.8*	82.9	*81.9*	82.9	*81.6*	83.1	*82.1*	83.2	*82.2*	83.1	*82.3*	83.4
October	*77.2*	80.2	*76.4*	79.4	*77.8*	80.3	*78.5*	80.7	*79.1*	81.3	*80.2*	81.6	*80.1*	81.8	*79.6*	81.5
November	*77.2*	76.3	*70.4*	74 7	*72.8*	76.7	*74.0*	77.5	*75.1*	77.9	*76.5*	78 5	*76.9*	79.5	*75.8*	78.8
December	*69.3*	70.7	*65.4*	70.7	*69.8*	74.2	*70.9*	75.0	*71.7*	74.5	*73.8*	75.9	*75.2*	77.7	*73.3*	76.5

NOTE.—From Charts 115–126, Atlas of Climatic Charts of the Oceans, U. S. Department of Commerce, Weather Bureau.

age sea surface and air temperatures for the 12 months of the year, the Gulf being divided into eight 5° quadrangles. This information was taken from charts 115 to 126 of the Weather Bureau's Atlas of Climatic Charts of the Oceans.

Probably the most recently prepared charts showing average sea surface temperatures in the Gulf are those of Fuglister (1947). Isotherms reproduced from his work for the winter month of February and the summer month of August are shown in figures 39 and 40. The main feature of the average winter pattern is a gradual drop from approximately 75° F. in the south to 65° F. in the north in all parts of the Gulf, the gradient being larger in the east portion. In the summertime the average temperatures are very nearly uniform at 84° F. throughout the region. Cruises of the *Alaska* indicate that considerable deviation from these average isotherms may occur at certain times.

The annual range of normal sea surface temperature varies from 15° to 20° F. in the northern portion of the Gulf, while in the central and southern portions the range is about 10° F. February is normally the coolest month of the year, though January is the coolest month for that portion of the Gulf adjacent to Texas and Mexico. Except for a few scattered areas, August is normally the warmest month of the year.

In regard to diurnal variation of surface temperature in the Gulf, a study by Stommel and Woodcock (1951) presents some data and discusses various methods of computation. It makes recommendations for future investigation of this problem.

According to Storey (Gunter 1947), there were nine freezes along the west coast of Florida between 1886 and 1936 which killed fishes in large numbers. Intense cold spells, sufficiently severe to kill large numbers of fishes, occurred along the Texas coast on an average of one every 14 years between 1856 and 1940, with less damaging spells coming at shorter intervals. Similar data for other parts of the Gulf coast are not available.

Slocum (1934–36) has made a comparative study of sea surface temperatures for various regions of the Gulf in different years. This study is based on temperature observations taken from 1912 to 1933. The year-to-year changes are summarized in table 2 for the regions shown by

TABLE 2.—*Some variations of mean annual sea surface temperatures for 1912–33* [1] *in various regions of the Gulf* (° F.)

[After Slocum]

Variation	(1) 25–26° N. 84–86° W.	(2) 27–29° N. 90–93° W.	(3) 26–28° N. 86–89° W.	(4) 21–25° N. 90–94° W.	(5) 23–24° N. 82–84° W.	(6) 21–22° N., 85–87° W. 22–23° N., 84–87° W.
High	79.5	77.0	78.7	79.7	80.9	81.1
Dif.	1.1	1.5	0.9	1.2	1.0	0.8
Mean	78.4	75.5	77.8	78.5	79.9	80.3
Dif.	1.6	1.6	1.2	0.9	2.1	1.0
Low	76.8	73.9	76.6	77.6	77.8	79.3
High-Low Dif.	2.7	3.1	2.1	2.1	3.1	1.8

[1] The number of observations varies from year to year. Few observations were made in 1917–19. In other years, the number ranged from 100 to over a thousand in each region. Locations are shown in figure 41.

encircled numbers in figure 41. The mean temperature for each year has been computed. It is of interest to note that in one case the minimum mean yearly temperature for a given region for this period of years differed from the overall mean temperature for the region by 2.1° F. Moreover, the maximum and minimum mean yearly temperatures differ by 3.1° F. in two localities. For one of these extreme examples, in the region 27–29° N., 90–93° W., the lowest mean yearly temperature recorded was for the year 1915 which showed a mean temperature of 73.9° F. In 1922 and 1927, the highest mean temperatures were recorded here, being 77.0° F. For the other example, the low was 77.8° F., the high 80.9° F. Slocum's study also included consideration of the means for the different months of the year.

SEA TEMPERATURE VARIATIONS WITH DEPTH

The sea temperatures obtained by the *Mabel Taylor* below the surface have been published by Parr (1935). Although the depths of these observations are not known accurately, they do give considerable information about vertical temperature distribution. An average temperature-salinity correlation in the Gulf of Mexico proper as worked out by Parr for the months February–April is given as table 3.

In the early 1940's the United States Navy developed the bathythermograph for making observations of sea temperature continuously from the surface to depths as great as 900 feet. To date, some 10,000 observations or bathythermograms have been made in the Gulf. Copies of these are now filed at the Woods Hole Oceanographic Institution where they are processed and in the Department of Oceanography at Texas Agricultural and Mechanical College. Their distribution by 1° quadrangles is shown in figure 42.

TABLE 3.—*An average temperature-salinity correlation for the Gulf of Mexico proper*

[After Parr]

Average temperature	Average salinity	Weighted average depth
° C.	°/∞	m.
24.74	36.19	5
23.06	36.06	15
21.03	36.14	58
19.25	36.28	94
17.09	36.22	125
14.85	35.95	192
13.00	35.68	237
10.89	35.35	321
9.60	35.16	380
8.57	35.04	432
7.42	34.93	562
6.39	34.88	647

Two bathythermograms, one for summer and the other for winter, were chosen from each of four parts of the Gulf within the 1,000-fathom line. These locations are indicated by encircled crosses in figure 41. The bathythermograms were chosen as being typical after considering range of temperature variation, general shape of temperature-depth curve, depth of thermocline, and other features. Unfortunately, due to the paucity of observations it was not possible at any one of the four positions to obtain "typical" summer and winter bathythermograms from the same year. However, by plotting a typical summer and a typical winter bathythermogram for each position on the same coordinates it was possible to show in a general

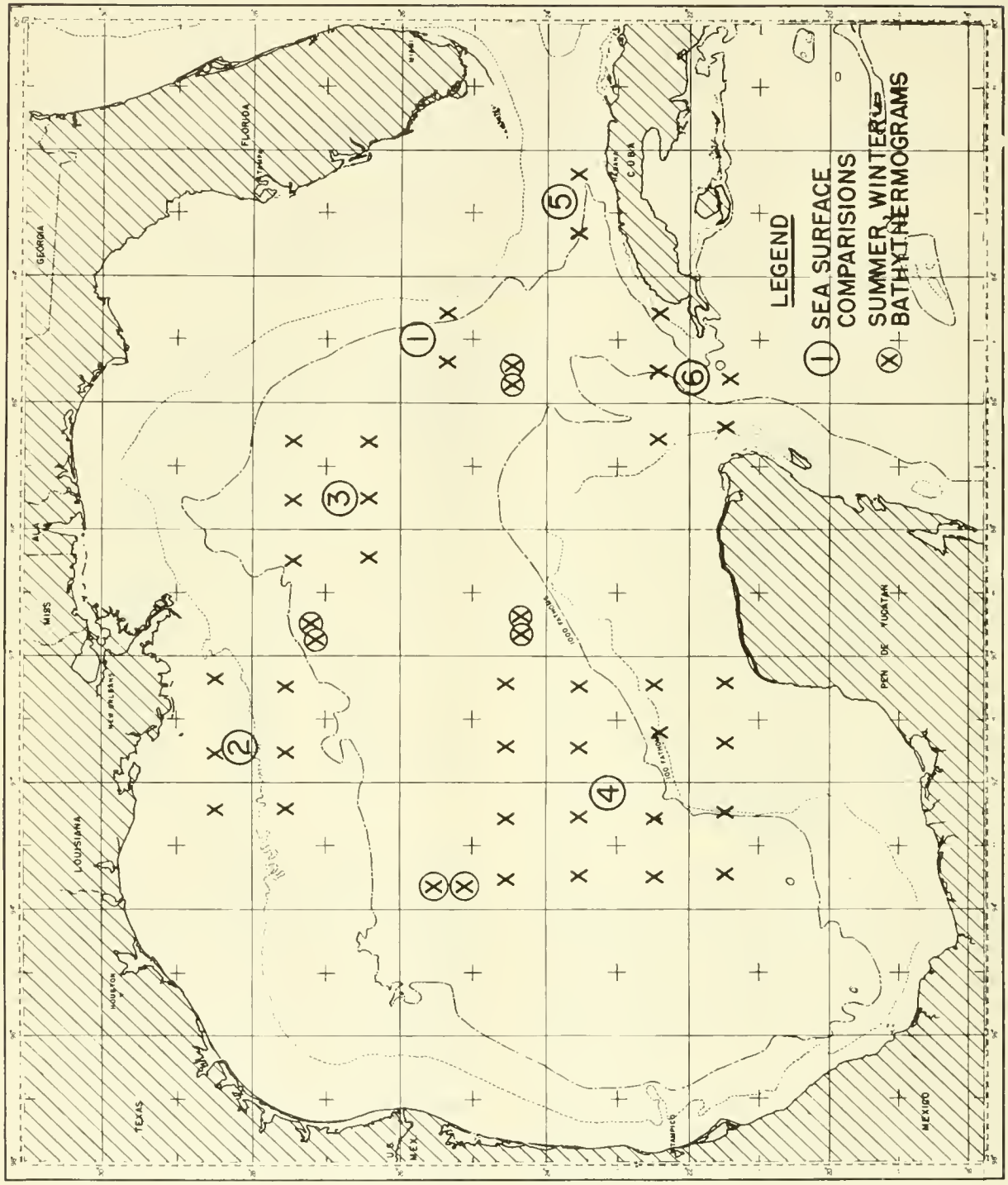

FIGURE 41.—Regions where comparative studies of sea temperatures were made.

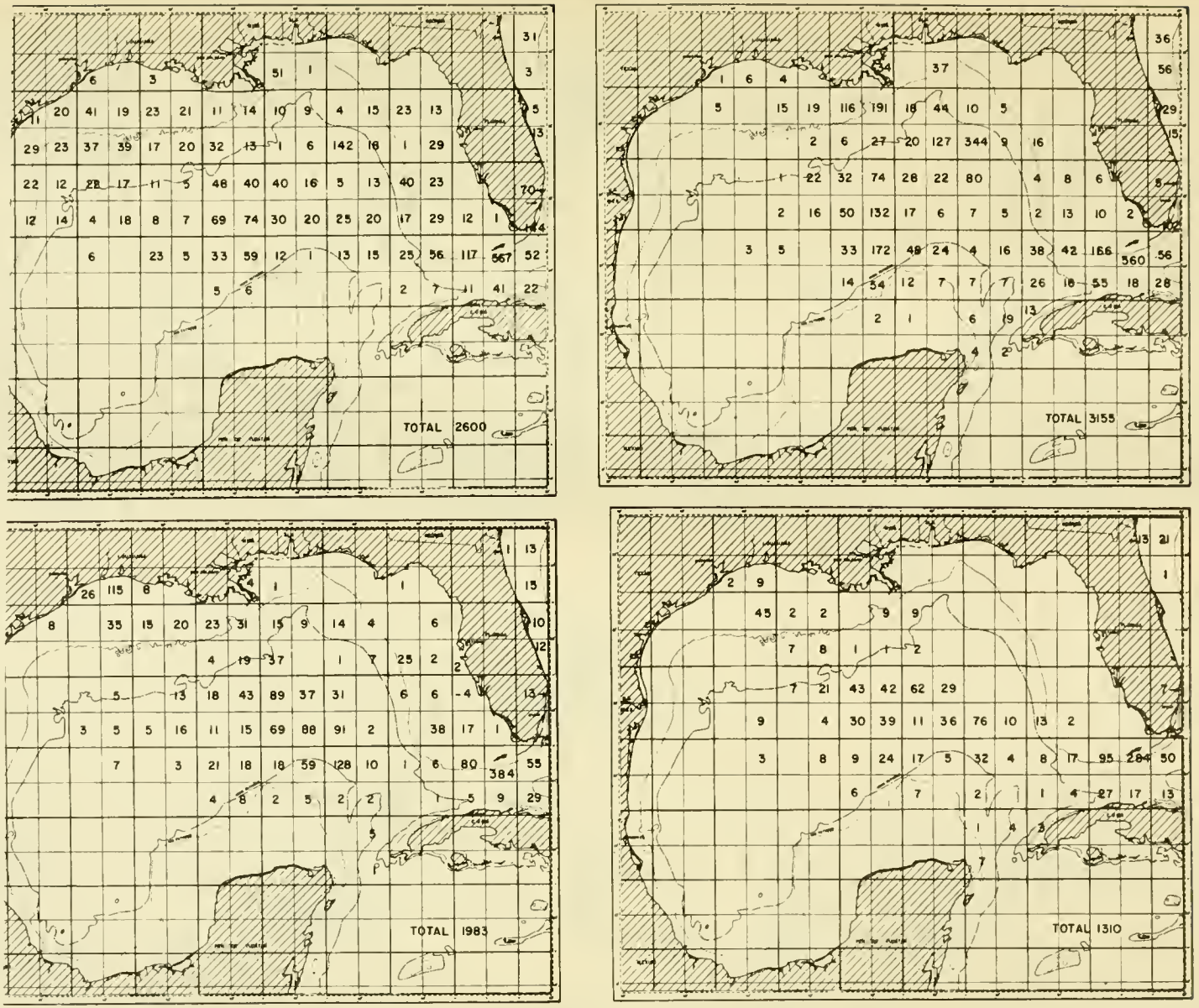

FIGURE 42.—(Upper left) Distribution of available bathythermograms January, February, March, 1941 through 1949. (Upper right) Distribution of available bathythermograms April, May, June, 1941 through 1949. (Lower left) Distribution of available bathythermograms July, August, September, 1941 through 1949. (Lower right) Distribution of available bathythermograms October, November, December, 1941 through 1949.

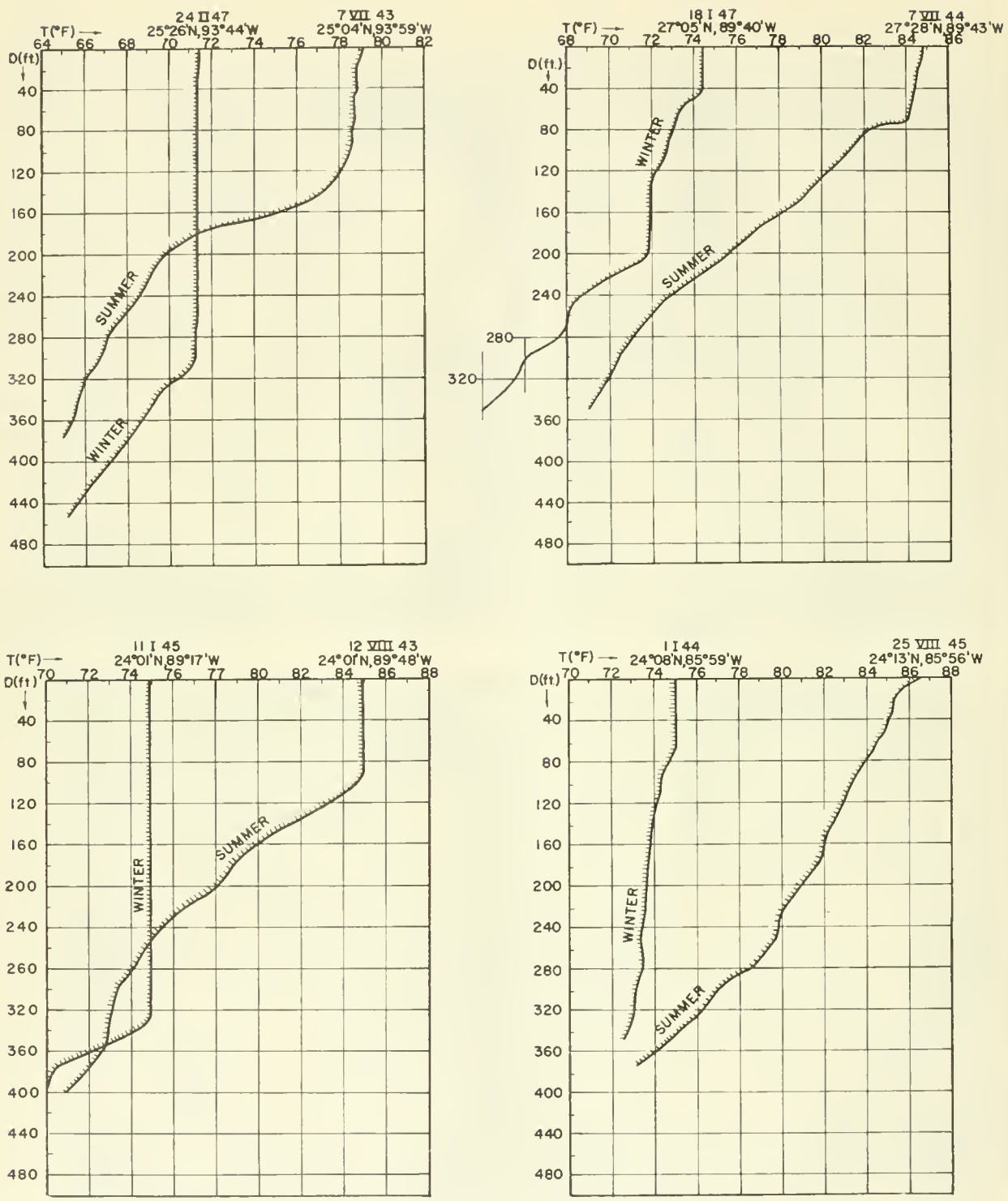

FIGURE 43.—Typical summer and winter bathythermograms from different areas in the Gulf of Mexico.

way the seasonal differences. These curves are presented in figure 43 which gives the date and position of each observation. Typical curves properly selected are believed more representative of conditions than average ones, since certain characteristic features of temperature structure may be lost in the process of averaging. A report by Adams and Sorgnit (1951) gives similar information for each 1° quadrangle of the Gulf where data were available. It also shows the contours of the bottom of the mixed or isothermal layer in summer and winter insofar as can be determined.

SALINITY

Parr (1935) presents a chart of the distribution of average salinities in the upper 50 meters of the Gulf of Mexico. It shows the values to be typically 36.00 parts per thousand over the entire central region. Water from the Mississippi River reaches to depths of 50 meters and extends beyond *Mabel Taylor* station 1106 (fig. 36), a distance of 150 miles, keeping salinities below 36.00 parts per thousand. Near stations 1201 and 1202 the river extends its influence on salinity only about 85 miles seaward.

From the Yucatán Channel a subsurface intrusion of water having salinity over 36.50 parts per thousand extends north and bends westward to the central part of the Gulf. From February to April this tongue underwent a marked shift westward in position of some 120 miles according to the *Mabel Taylor* data.

Above 50 meters waters of salinity greater than 36.25 parts per thousand are found over both the wide Campeche and Florida Banks indicating possible upwelling of the subsurface intrusion.

Average variation of salinity with depth is shown in table 3.

TEMPERATURE-SALINITY RELATIONSHIPS

An average temperature-salinity relationship for the Gulf proper was shown in table 3. A single station typical of what Parr defined as the Gulf Complex is *Mabel Taylor* station 705 (fig. 36). Another which he calls typical of the Caribbean Complex, divided from the Gulf Complex by a line extending from the northeast corner of Yucatán Bank to the southwest corner of the Florida Bank, is station 701 (fig. 36). Data for these stations are listed in table 4. The primary difference between these two distributions is that at temperatures above 18° C. the Gulf Complex station has markedly lower salinities, being below 36.32 parts per thousand, while the Caribbean station has values as high as 36.73 parts per thousand.

The T–S curves in the Yucatán Channel do not seem to vary significantly from year to year, but those in the Straits of Florida are not so stable, particularly at temperatures above 20° C. Cruises in different years in the Straits have shown wide variations in the extent of Gulf water found in the upper 200 meters.

TABLE 4.—*Typical temperature and salinity data*

[After Parr]

Gulf Complex Station 705, Feb. 18, 27°42′ N., 86°00′ W.			Caribbean Complex Station 701, Feb. 16, 23°28′ N., 85°37′ W.		
Depth	Salinity	Temperature	Depth	Salinity	Temperature
m.	‰	° C.	m.	‰	° C.
0	35.52	23.75	0	36.18	25.34
30	36.15	23.15	100	36.32	25.28
100	36.32	18.59	200	36.73	21.88
150	36.21	16.58	300	36.44	18.21
200	35.96	14.94	400	35.94	14.96
300	35.52	12.30	600	35.08	9.12
500	35.08	7.88	800	34.86	6.86
700	34.87	5.91	1,000	----------	5.15
900	34.92	4.94			
1,200	34.95	4.21			
1,500	34.97	4.21			
2,000	34.97	4.16			
2,500	34.97	4.22			
3,000	34.97	4.24			

Parr (1935) believes that since—

> The presence of Gulf waters in the Straits of Florida is . . . identified with the location in which a countercurrent running in the opposite direction of the Caribbean-Florida Current flow is usually indicated on the hydrographic charts. . . . it seems reasonable to draw the tentative conclusion "the water masses of the Gulf of Mexico proper should be considered part of the coastal water system of the North and Central American Atlantic seaboard and not as part of the oceanic-circulation system of the Caribbean and Florida Currents."

Considerable further evidence is required to fully support this tentative conclusion.

Below 800–1,200 meters depth observations of the *Mabel Taylor* showed hydrographic conditions in the Gulf so extremely uniform that it was not considered advisable to attempt to prepare vertical profiles for the deep layers. More accurate depth determinations on subsequent investigations may bring out significant variations at these depths.

OCEAN WIND WAVES AND SWELL

A basic and easily obtainable reference for climatic data on waves in the Gulf is the Atlas of Sea and Swell Charts of the United States Navy Hydrographic Office (1943–50), Miscellaneous Publication No. 10,712, A through D. Certain uses of these data are discussed by Fleming and Bates (1951).

Information concerning wave heights in some regions on certain specific days may be obtained by referring to wind data available through the United States Weather Bureau and applying a method of calculation described in United States Navy Hydrographic Office Publication No. 604, Techniques for Forecasting Wind Waves and Swell.

The problem of wave action on structures is discussed by Munk (1947). Considerable additional research will be required before knowledge of wave forces in the Gulf is complete. Such work has been underway at the University of California (La Jolla and Berkeley) and is being initiated at Texas Agricultural and Mechanical College.

SHALLOW WATER OCEANOGRAPHY

Much of the marine interest on the Gulf coast tends to center on the shallow waters. There are many bays, lagoons, and inlets of great importance to fishing, navigation, recreation, oil recovery, and other activities. Each of these presents its own peculiar problems, and extensive investigations have been carried on in many of them. A recent publication indicating the nature of this work is that of Collier and Hedgpeth (1950). A good bibliography is included indicating the variety of studies which are important in determining the physical characteristics of such regions.

Many analyses of shallow water areas have been conducted for private sponsors, and the results are not yet available. However, they are gradually being released for publication.

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LIGHT PENETRATION IN THE GULF OF MEXICO

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Although the interest and study of submarine illumination has increased throughout the past years, there has not been a proportionate increase in investigation of this subject in the Gulf of Mexico. This paper will attempt to summarize the present knowledge and recent efforts in underwater illumination as applied to this area. It is hoped that the meagerness of the information will be an incentive to future endeavor.

The major part of the known data presented here was calculated from Secchi disc depths. Clarke (1941) points out that Secchi disc determinations are in reasonable accord with measurements obtained from the photronic photometer. The relationship of $K=1.7/D$, where "D" equals the depth in meters when the disc just disappears and "K" denotes the coefficient, was introduced by Poole and Atkins (1929) to convert Secchi disc values into extinction coefficients. The standard equation, $\frac{I}{I_0}=e^{-KL}$, where L is the depth of water expressed in meters in which the intensity of illumination is lowered from I_0 to I, is of advantage for further manipulation of the extinction coefficient.

Several institutions located in the area have studied illumination in the Gulf, but their figures are not yet available.

E. R. Fenimore Johnson, under the auspices of the Smithsonian Institution, conducted studies dealing with the translucence of water as related to visual and photographic transparency in the area under discussion. This information is at present being prepared for publication.

Table 1 represents submarine illumination data that are available at the time of writing. Source material marked WHOI represents information from the Woods Hole Oceanographic Institution's files; D indicates *Dana* reports (Schmidt 1929). The footnoted entries denote photronic photometer derived extinction coefficients.

Taylor (1928), in connection with his algal studies in the Dry Tortugas area, recorded data obtained from the Secchi disc. This information

TABLE 1.—*Submarine illumination data according to the Woods Hole Oceanographic Institution (WHOI) and* Dana *reports (D)*

Date	Latitude (N.)	Longitude (W.)	Secchi disc "K"	Source	Remarks
Feb. 1, 1922	21°49′	85°41′	0.077	D	Station 1221.
Mar. 22, 1938	23°13′	82°19′	[1].049	Series 460	0 to 100 M.
			[1].054	WHOI	89 to 150 M.
Feb. 4, 1922	23°13′	82°21′	.052	D	Station 1229.
Feb. 3, 1922	23°40′	82°31′	.065	D	Station 1227.
Aug. 27, 1943	24°25.8′	81°47.9′	<.11	WHOI	
Aug. 10, 1943	24°26.7′	81°57.7′	.35	WHOI	
Aug. 3, 1943	24°27.7′	81°48.1′	.146	WHOI	
Aug. 11, 1943	24°29.8′	81°48.3′	.265	WHOI	
Aug. 10, 1943	24°30.2′	81°48.3′	.35	WHOI	
Aug. 3, 1943	24°30.5′	81°48.3′	.144	WHOI	
No date	24°32′	81°48.5′	.33–[1].4	WHOI	
Aug. 7, 1943	24°32.8′	81°49′	.37	WHOI	
Aug. 9, 1943	24°39.9′	81°53.8′	.31	WHOI	
Aug. 6, 1943	24°48′	81°50′	.31	WHOI	
Aug. 6, 1943	24°50′	81°41′	.231	WHOI	
Feb 4, 1951	24°51′	85°58′	.074		Stetson Station,
Mar. 16, 1947	24°59′	87°47.5′	.09	WHOI	No. 1.
Aug. 4, 1943	25°03.5′	81°39.75′	.231	WHOI	
Feb. 24, 1947	25°24′	93°43′	.07	WHOI	
July 19, 1943	27°35.8′	82°55.6′	.124	WHOI	
July 19, 1943	27°36′	82°51.7′	.266	WHOI	
July 21, 1943	27°37.2′	82°39.2′	.464	WHOI	
Jan. 26, 1947	27°38′	93°53′	.08	WHOI	
July 21, 1943	27°39.1′	82°36.6′	.62	WHOI	
July 22, 1943	27°45.4′	82°31.5′	.62	WHOI	
July 23, 1943	27°47.2′	82°32.4′	.62	WHOI	
July 22, 1943	27°48.5′	82°34.7′	.699	WHOI	
July 26, 1943	27°50′	96°27′	.098	WHOI	
July 22, 1943	27°50.6′	82°33.7′	.62	WHOI	
July 27, 1943	28°00′	90°46.19′	.168	WHOI	
July 15, 1943	28°16′	96°18′	.14	WHOI	

See footnote at end of table.

TABLE 1.—*Submarine illumination data according to the Woods Hole Oceanographic Institution (WHOI) and* Dana *reports (D)*—Continued

Date	Latitude (N.)	Longitude (W.)	Secchi disc "K"	Source	Remarks
July 25, 1943	28°17′	96°15′	14	WHOI	
Apr. 25, 1945	28°35.6′	90°03′	.28	WHOI	
Apr. 20, 1945	28°37.2′	89°46′	.35	WHOI	
Oct. 5, 1942	28°43′	95°20′	.174	WHOI	
Apr. 13, 1945	28°51.6′	89°39′	12 1	WHOI	
Apr. 13, 1945	28°53′	89°33′	12 1	WHOI	
July 15, 1943	28°54′	95 14′	1 39	WHOI	
Apr. 20, 1945	28°54 8′	89°34′	1 6	WHOI	
July 19, 1943	28°55.3′	95°15.7′	1.39	WHOI	
July 5, 1943	29°02′	94°45′	1 86	WHOI	
Apr. 10, 1937	29°08′	88°39′	[1] 16	WHOI	2 to 6 M.
			[1] 88	Series 441	6 to 24 M.
			[1] .058	do	24 to 81 M
Mar. 29, 1945	29°09′	88°56′	11 3	WHOI	
Apr. 11, 1937	29°14′	87°48.5′	[1] .054	WHOI	2 to 95 M.
			[1] .039	Series 442	95 to 169 M.
			[1] .047	do	Average 2 to 169 M.
Apr. 9, 1937	29°16′	88°50′	19	WHOI	2 to 6 M.
			.10	Series 440	20 to 53 M.
Mar. 29, 1945	29°24′	88°01′	.74	WHOI	
Apr. 9, 1937	29°27′	88°48′	[1] .22	Series 439	2 to 25 M.
July 10, 1943	29°29′	93°41′	23	WHOI	
No date	29°30′	94°80′	1.90	WHOI	
Aug. 10, 1943	29°41′	94°59′	5.60	WHOI	
June, July (no date)	29°42′	93°52′	1 4–5.7	WHOI	
Aug. 10, 1943	29°42 33′	94°59.25′	5.60	WHOI	
Aug. 10, 1943	29°42.5′	95°01.25′	5.60	WHOI	
June–September 1943	30°35′	88°00′	.19–1 9	WHOI	

[1] Photronic photometer derived extinction coefficients

was reported as the depth in which the disc disappeared. These are converted here into extinction coefficients These values are entered in table 2. More detailed information for 51 values in this area is tabulated in the same paper by Taylor.

TABLE 2.—*Extinction coefficients of the Dry Tortugas area based on locations and data of Taylor (1928)*

Station	Secchi disc "K"
Lagoon	0 227–0 134
Outside of reefs	.207– .121
Outside island group	.089– .064
Gulf Stream (15 to 20 miles offshore)	067– .047
East of Loggerhead Key	.189– 150
West end of Garden Key Channel	227– .174

Clarke (1938) calculated the extinction coefficients for a series of stations east of the Mississippi Delta. These values are indicated in table 1 as series 439 through 442.

For security reasons, Hulburt's paper (1940) on transparency and visibility of submerged objects in the Key West sector has been classified.

Bumpus and Clarke (1947) have connected equal points of known "K" values on a chart which includes the Gulf of Mexico. It must be remembered that these lines are based on very few observations, and considerable interpolation was necessary.

The Special Scientific Reports, Fisheries No. 8, by Butler (1949), and No. 14, by Butler and Engle (1950), of the United States Department of the Interior contain turbidity indices for selected points of the Mississippi Sound and Lake Pontchartrain. Turbidity is expressed as the percentage–transmission of light through the sample. No correlations with extinction coefficient values or direct Secchi disc measurements are presented.

It is obvious that the transparency data for the Gulf of Mexico are quite inadequate to meet the increasing demands of researchers.

It is admitted that the Photronic photometer is more accurate than the Secchi disc methods of determining the extinction coefficients, but it is also more time consuming. It is suggested, therefore, that the Secchi disc be used. Not more than 2 or 3 minutes are required to lower the white disc (usually 20 or 25 cm. in diameter) until it disappears, and to record the depth. The whole operation is simple and can readily be carried out by unskilled persons.

In view of the limited transparency observations in the Gulf of Mexico it would be difficult to draw accurate comparisons with other areas.

I am indebted to many members of the staffs of the Woods Hole Oceanographic Institution and the University of Miami Marine Laboratory, in particular to Dean F. Bumpus and H. B. Moore for placing their files at my disposal.

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DISTRIBUTION OF CHEMICAL CONSTITUENTS OF SEA WATER IN THE GULF OF MEXICO[1]

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Earliest records of chemical analyses of Gulf of Mexico waters were published by biologists and biochemists who studied the sea water composition as one ecological factor in the complex environment of the marine organisms with which they were concerned. Much of this early work was centered at the Carnegie Institution laboratory at the Dry Tortugas near the western end of the Florida Keys. First oceanographical studies of the chemistry of the water were confined to the system of currents flowing across the southeastern corner of the Gulf from the Yucatán Channel to the Straits of Florida. Practically all analyses of offshore and subsurface waters of the Gulf were made in 1914, 1922, 1932, 1934–39, 1942, and since 1947.

The chemical data are summarized here in order of the decreasing amount of published information: salinity, oxygen, phosphorus, nitrate, nitrite, pH, alkalinity and carbon dioxide components, copper, and miscellaneous chemical constituents.

SALINITY

Salinity is defined as the total amount of dissolved solid material in grams contained in 1 kilogram of sea water when all the carbonate has been converted to oxide, the bromine and iodine replaced by chlorine, and all organic matter completely oxidized. In practice, it is calculated from the chlorinity which is determined by titration with silver nitrate solution. Less accurate salinity values are calculated from densities determined with hydrometers. Both salinity and chlorinity are reported as parts per thousand by weight, using the symbol, °/₀₀.

In the shallow waters of the Dry Tortugas, in the years 1910 to 1913, Dole (1914) reported salinities ranging from 35.41°/₀₀ to 36.11°/₀₀. Diurnal and tidal changes in salinity in the same area in 1919 indicated a wider range, 34.61°/₀₀ to 36.29°/₀₀ (Wells 1922).

In the bays along the coast of Texas the wide salinity variations cause recurring mass mortality of marine animals. This situation was reported by Johnson (1882), Rathbun (1895), and Higgins and Lord (1926). Results of detailed surveys of the salinity distribution in the Texas bays in 1926–27 were reported by Galtsoff (1931). Additional studies of salinity along the Texas, Louisiana, and Mississippi coasts were published by Higgins (1931), Riley (1937), Lindner (1939, 1941), Gunter (1945, 1947, 1950), Wise, Winston, and Culli (1945), Price (1947), Geyer (1950), and Collier and Hedgpeth (1950). Alternating floods and droughts cause salinity changes from nearly fresh to 100°/₀₀, three times that of normal sea water.

In connection with studies of the red tide along the west coast of Florida, salinity data were published by Galtsoff (1948), Gunter, Williams, Davis, and Smith (1948), and Ketchum and Keen (1948). In the open Gulf salinities ranged from 30.6°/₀₀ to 37.0°/₀₀; in Estero Bay, 21.4°/₀₀; and near the mouth of the Caloosahatchee River, 12.2°/₀₀.

In connection with plankton studies in 28 mangrove-bordered inland bodies of brackish water on the west and south coasts of Florida in 1947–48, Davis and Williams (1950) reported salinities ranging from 0.61°/₀₀ to 29.09°/₀₀.

The present center of Florida's oyster industry, Apalachicola Bay in northwest Florida, was the subject of an 18-month survey of salinity (Ingle 1951; Ingle and Dawson 1951). Annual variations ranged from fresh water to 42.5°/₀₀ Daily, weekly, and tidal variations were considerable.

Apparently the first published salinity records for offshore and subsurface Gulf of Mexico waters are those of Vaughan (1918) who reported salinity values for samples collected at five stations between Havana and Key West from the surface to

[1] Contribution No. 101, from the Marine Laboratory, University of Miami.

1,700 meters by the United States Coast and Geodetic Survey steamer *Bache* in March 1914. Salinities of two surface samples collected a little farther east in January and February 1919 were reported by Mayor (1922). Stations taken by the Danish research vessel *Dana* across the Havana section in 1922 provided data for a salinity profile (Nielsen 1925; Schmidt 1929; Jacobsen 1929). Composition of two surface samples collected in July 1922 in the Gulf Stream south of the Dry Tortugas was reported by Lipman (1929).

The Havana section was studied again in February 1932 on the Yale Oceanographic Expedition aboard the schooner *Mabel Taylor* (Parr 1935). Expeditions from the Woods Hole Oceanographic Institution aboard the research vessel *Atlantis* have made studies of the Havana section in March 1934 (Bulletin Hydrographique, 1935), February and April 1935 (Bulletin Hydrographique, 1936; Seiwell 1938), March 1938 (Montgomery 1941), and May 1939 (Riley 1939). The vertical distributions of salinities across the Havana sections in 1922, 1932, and 1934 were summarized in profiles by Parr (1935, pp. 42–44, 71). Below 100 meters the isohalines generally sloped downward toward the Cuban coast. In the middle of the Straits the salinity generally increased from 35.83°/₀₀ at the surface to 36.68°/₀₀ at 200 meters, then decreased to a minimum of 34.87°/₀₀ at 800 meters, and thereafter increased only slightly to 34.97°/₀₀ at 1,600 meters.

The next most thoroughly studied part of the Gulf of Mexico is the Yucatán Channel where the Caribbean Current enters the Gulf between western Cuba and Mexico. This section was studied in 1922 from the *Dana* (Schmidt 1929; Jacobsen 1929), in February 1932 from the *Mabel Taylor* (Parr 1935), and from the *Atlantis* in May 1933 (Bulletin Hydrographique, 1934; Parr 1937; Rakestraw and Smith 1937) and March 1934 (Bulletin Hydrographique, 1935; Parr 1937). The vertical distributions of salinities across the Yucatán Channel in 1933 and 1934 were summarized in profiles by Parr (1937, pp. 42–43). Here, also, the isohalines generally sloped downward toward the Cuban coast. The vertical distribution of salinity was similar to that described above for the Havana section. Comparison of the average temperature–salinity correlation curves for the Yucatán Channel and the Havana section of the Straits of Florida led Parr (1935) to conclude that the water mass entering the Straits of Florida is identical with that which passed through the Yucatán Channel except for a very small layer of "Gulf type" water at the surface on the left (Florida) side of the main current.

Parr's (1935) report on the expedition of the *Mabel Taylor*, February to April 1932, included a map showing the locations of the 68 stations occupied in the Gulf, complete temperature and salinity data, salinity profiles of 5 sections across the main parts of the Gulf, maps of salinity distribution in upper 50 meters and at 200 meters, graphs of vertical distribution of salinity, and temperature-salinity correlation curves. The expedition was not provided with unprotected reversing thermometers and therefore had no means for accurate determination of the depths of observations. The highest salinities (above 36.25°/₀₀) in the upper 50 meters were found in the shallow waters off the west coast of Florida and the Campeche Bank. Most of the offshore water in this surface layer had salinities between 36.00°/₀₀ and 36.25°/₀₀. Low salinities (below 33°/₀₀) were found along most of the northern regions of the Gulf, and very low (less than 24°/₀₀) salinities were found near the mouth of the Mississippi River and to the west from the delta region. At a typical station in the western Gulf (25°46′ N., 92°31′ W.) the salinity decreased slightly from 36.16°/₀₀ at the surface to 36.12°/₀₀ at 50 meters, then increased to the maximum of 36.31°/₀₀ at 100 meters, then decreased to the minimum of 34.87°/₀₀ at 600 meters, then increased slightly to 34.92°/₀₀ at 800 meters, below which it remained practically constant down to 3,000 meters.

Dietrich (1939, p. 119) used the 1932 data from the Gulf of Mexico to prepare another map showing the distribution of the maximum salinities, regardless of depth. This showed a continuous layer of high salinity (above 36.7°/₀₀) water in most of the Caribbean Sea, the northern half of the Cayman Sea, and extending northward into the Gulf to 26°00′ N. and 89°20′ W.

The *Atlantis* occupied stations along several sections of the central and western Gulf in February to April 1935 (Bulletin Hydrographique, 1936). A map showing the locations of these stations was published by Vaughan (1937, p. 21). Vertical distribution of salinity at a typical station in April 1935 in the western Gulf (25°40′ N.,

94°23′ W.) was charted by Dietrich (1939, p. 117, fig. 33); it was similar to that described above for the *Mabel Taylor* station about 100 miles farther east.

The *Atlantis* occupied a series of nine stations in the northeast Gulf in March and April 1942 from which salinity data were published (Bulletin Hydrographique, 1950). The same vessel occupied a series of 24 stations in the northwestern and central Gulf, January to March 1947 (Trask, Phleger, and Stetson, 1947).[1]

The research vessel of the Fish and Wildlife Service laboratory at Sarasota, Florida, has occupied stations from Sarasota to Naples and to a distance of 120 miles off shore at approximately monthly intervals since May 1949. Chemical analyses of the water were made for chlorinity, dissolved oxygen, inorganic phosphate, total phosphorus, nitrate, nitrite, and hydrogen ion concentration.[2] The phosphorus data have been published (Graham, Amison, and Marvin, 1954). The other data will be published later.[3]

The Fish and Wildlife Service research vessel *Alaska* began a series of oceanographic cruises in the Gulf of Mexico in 1951. Salinities collected on these cruises are being determined at Texas Agricultural and Mechanical College. They shortly will be made available in a mimeographed form.[4]

DISSOLVED OXYGEN

The first available data on dissolved oxygen content of Gulf of Mexico water seem to be on the results of analyses of water collected at the Dry Tortugas and published by McClendon (1918).

Oxygen determinations were reported when the *Atlantis* occupied stations across the Yucatán Channel in May 1933, March 1934, and February 1935; across the Havana section of the Florida Straits in March 1934, February and April 1935, August 1938, and May 1939; and in the main part of the Gulf in February to April 1935. The oxygen and other data from most of these stations were published in the Bulletin Hydrographique in 1934, 1935, and 1936. A graph of the vertical distribution of dissolved oxygen in the center of the Yucatán Channel in 1933 was given by Rakestraw and Smith (1937, p. 9), and a map showing the locations of the stations was published by Vaughan (1937, pl. 11).

Seiwell summarized the oxygen data from the 1933–1935 *Atlantis* stations in the eastern half of the Gulf with profiles across the Straits of Florida and the Yucatán Channel (Seiwell 1938, figs. 6, 15) and gave charts of the horizontal distribution of oxygen at 100, 250, 500, 750, 1,000, 1,500, and 2,500 meters (Seiwell 1938, figs. 7, 8, 11, 14, 16, 17, 20). Vertical distribution of oxygen at a typical station in the western Gulf (25°40′ N., 94°23′ W.) was charted by Dietrich (1939, p. 117, fig. 33): from about 4.8 cubic centimeters per liter at the surface, it increased slightly to about 4.9 cubic centimeters at 25 meters, then decreased to a minimum of 2.35 cubic centimeters at 300 meters, then increased gradually to about 5.0 cubic centimeters at 2,400 meters, and thereafter remained constant to 3,400 meters. Dietrich (1939, p. 120, fig. 35) also presented a chart showing the distribution of minimum oxygen concentration, regardless of depth, in all but the southwest part of the Gulf. The lowest oxygen concentrations (below 2.5 cc. per liter) were found in the northwest corner; values below 2.7 cc. per liter were observed north of the Campeche Bank and off the central west coast of Florida.

Riley (1938, 1939) reported oxygen concentrations in surface and subsurface samples in the summer of 1938 at two stations in the Dry Tortugas in depths of 3 and 19 meters, one station in the Florida Straits in the depth of 166 meters, and from two stations in the Havana section of the Florida Straits in May 1939. In presenting a detailed summary of oxygen in the Atlantic Ocean he omitted the Gulf of Mexico (Riley 1951).

Scattered records of oxygen analyses made in connection with studies of animal mortality including the red tide have been published by Gunter (1942), Galtsoff (1948), Gunter, Williams, Davis, and Smith (1948), Connell and Cross (1950).

PHOSPHORUS

The earliest published record of phosphorus content of Gulf of Mexico water is that of Lipman

[1] Salinity data from these stations were kindly supplied by Fred B. Phleger on August 15, 1950. They are also available from data cards on file at the Woods Hole Oceanographic Institution and will probably be published in the Bulletin Hydrographique.

[2] Personal communication from L. A. Walford, December 5, 1950.

[3] Personal communication from Herbert W. Graham, January 3, 1952.

[4] Temperature-salinity relationships are discussed in the article of D. F. Leipper, Physical Oceanography of the Gulf of Mexico, in this book, pp. 119–135.

(1929) who reported results of analyses of two samples of water collected at the Dry Tortugas in July 1922: 1.00 and 4.80 parts phosphate per million parts of water (10.5 and 50 microgram-atoms phosphate-phosphorus per liter).

Information on the vertical distribution of phosphorus in the Gulf of Mexico is very limited. Determinations of phosphate were made on the 16 samples (surface to 1,732 meters) collected at *Atlantis* station 1606 in the middle of the Yucatán Channel in May 1933 (Bulletin Hydrographique, 1934, p. 103). Graphs of the vertical distribution of phosphorus at this station were published by Rakestraw (1936, p. 160, fig. 11) and Rakestraw and Smith (1937, p. 9, fig. 7).[5] The phosphate-phosphorus[6] remained nearly constant at 0.15 μg-atoms/L from the surface to 97 meters, then increased to a maximum of 2.47 at 736 meters, then decreased to 1.71 at 1,732 meters. These data for Yucatán Channel water were used in the charts of horizontal distribution of phosphate at various depths (Rakestraw and Smith, 1937, figs. 10–12).

Horizontal and vertical distribution of phosphate near the mouth of the Mississippi River in March 1937 was reported in tables and a map by Riley (1937, pp. 74, 63). He found about 0.58 μg-atoms/L in the low salinity surface water at the station at the mouth of the river. Phosphate decreased in all directions to an average of 0.14 μg-atoms/L at the stations in the Gulf.

Distribution of phosphate at the Dry Tortugas and in the Florida Straits was reported by Riley (1938, 1939) and Riley, Stommel, and Bumpus (1949, p. 16). Near Loggerhead Key where the depth was 3 meters, the phosphate ranged from 0.015 to 0.10 μg-atoms/L from July 18 to August 2, 1938. At his station midway between Loggerhead and Garden Keys where the depth was 19 meters the phosphate at depths of 1, 5, 10, and 15 meters varied quite differently with depth on 4 days in July 1938 from 0.02 to 0.16 μg-atoms/L. His data from other stations are summarized in table 1.

Riley (1951) presented a detailed summary of phosphorus distribution in the Atlantic Ocean but omitted the Gulf of Mexico, except for his discussion (p. 15) of the tendency for the products of regeneration (phosphate and nitrate) to accumulate in the deep water of the Caribbean-Gulf of Mexico basins because the outflow through the Straits of Florida is shallower than the maximum depth of the inflowing water.

TABLE 1.—*Vertical distribution of phosphate (μg-atoms/L) in the Florida Straits*

Location	Station depth (meters)	Date	Levels below surface at which samples were taken (in meters)							
			1	18	45	90	100	153	200	300
20 miles south of Loggerhead Key	166	Aug. 6, 1938	0.11	0.02	0.12	0.12	------	1.07	------	------
Midway between Havana and Key West. Station number 3491	1,719	May 15, 1939	.03	------	------	------	0.07	------	0.33	0.68
Off Matanzas, Cuba, Station number 3486	722	May 11, 1939	.21	------	------	------	.10	------	.51	------

Results of phosphate analyses at various inshore stations in the Tampa Bay area and near the southern tip of the Florida peninsula in 1946, reported by Williams (1947) and Smith (1949), are summarized in table 2.

TABLE 2.—*Phosphate (μg-atoms/L) along Gulf coast of Florida in 1946*

Area	Location of sampling station	Date	Phosphate μg-atoms/L
Tampa Bay	Green Key, Hillsboro Bay	Jan. 30	8.4
Do	do	June 4	12.0
Do	1 mile west of Green Key	do	8.4
Do	Terra Ceia Bay	Jan. 29	.84
Do	Terra Ceia Bay (center)	June 3	3.60
Do	Terra Ceia Bay (north side)	do	4.80
Cape Sable	¼ mile southwest of Catfish Key, Florida Bay.	Mar. 9	.03
Do	Conchie Channel, Florida Bay	do	.03
Do	East River, east of Whitewater Bay.	May 6	.03

In connection with studies of the red tide along the Gulf coast of Florida in 1947 made during and

[5] There appears to be some confusion regarding units in the three publications dealing with this phosphorus data. The raw data in the Bulletin Hydrographique are reported in milligrams phosphate per cubic meter. When these figures are divided by 95, the corresponding unit is milligram-atoms per cubic meter or microgram-atoms per liter. The scale for fig. 11, p. 160 of Rakestraw (1936) indicates phosphate from 0 to 1.5 microgram-atoms per liter, but the scale for fig. 7, p. 9 of Rakestraw and Smith (1937) indicates phosphate from 0 to 3 milligram-atoms per liter. It is believed that the units in the last paper should be either microgram-atoms per liter or milligram-atoms per cubic meter, which are numerically equal. Later papers report this same data in microgram-atoms per liter (Sverdrup, Johnson, and Fleming, 1942, p. 241) or milligram-atoms per cubic meter (Riley, Stommel, and Bumpus, 1949; Riley, 1951).

[6] Phosphate data reported in this section have been corrected for salt error by multiplying any uncorrected values by 1.15 (Cooper 1938, p. 177; Robinson and Thompson 1948, p. 36).

after the blooming of *Gymnodinium brevis*, the concentrations of inorganic phosphorus were found as high as 7.4 μg-atoms/L and total phosphorus (particulate organic, dissolved organic, and inorganic) up to 20.4 μg-atoms/L in the amber colored water (Ketchum and Keen 1948, p. 18; Gunter, Williams, Davis, and Smith, 1948, p. 319: Galtsoff 1948, p. 20; Smith 1949, p. 5).

These unusually high phosphorus concentrations suggested the need for more detailed information on horizontal, vertical, and seasonal distribution of phosphorus compounds to clarify the fundamental causes of the red tide. Accordingly, when the research program of the Fish and Wildlife Service laboratory in Sarasota, Florida, was planned studies of the distribution of total, inorganic, and organic phosphorus were given primary attention. Results of a detailed survey at 13 stations in the rivers, along the middle Florida coast, and 120 miles west to the 100-fathom line from May 1949 to August 1950 have been published (Graham, Amison, and Marvin, 1954). They show a gradual decrease in phosphorus content of the surface water with increase in distance from shore. The phosphorus-rich waters discharged from the Peace River did not affect, however, the local Gulf waters to any measurable degree. Beyond 14 miles from shore the concentration of total phosphorus in the surface water was usually below 0.25 μg-atoms/L and inorganic phosphorus was usually below 0.10 μg-atoms/L. Larger quantities of phosphorus, mostly inorganic, were found at depths below 50 meters. Occasional upwelling did not seem to influence the phosphorus content of the euphotic zone. There was no evidence of the bottom sediments contributing any appreciable quantities of phosphorus to the water. Local concentrations of the planktonic blue-green alga, *Trichodesmium*, appeared to be associated with high concentrations of total phosphorus.

NITRATE-NITROGEN

Studies of nitrate distribution in the Gulf have generally paralleled those of phosphate reviewed above. Vertical distribution of nitrate in the middle of the Yucatán Channel in May 1933 (Bulletin Hydrographique, 1934, p. 103) was indicated in a graph by Rakestraw (1936, p. 160, fig. 11) and Rakestraw and Smith (1937, p. 9, fig. 7).[7] The nitrate decreased from 2.4 μg-atoms/L at the surface to 1.4 μg-atoms/L at 49 meters, then increased regularly to a maximum of 37.1 μg-atoms/L at 736 meters, then decreased to 24.2 μg-atoms/L at 1,732 meters. These data for Yucatán Channel water were used in the charts of horizontal distribution of nitrate at various depths (Rakestraw and Smith, 1937, figs. 14–16).

Although no nitrate determinations were made on Gulf waters near the mouth of the Mississippi, Riley (1937, p. 69) reported the following data (supplied by A. A. Hirsch of the New Orleans Sewerage and Water Board Company) which are 1935 average values for the Mississippi River water at New Orleans:

Ammonia nitrogen	20 mg/m³
Albuminoid nitrogen	350 mg/m³
Nitrite nitrogen	5 mg/m³
Nitrate nitrogen	200 mg/m³

Nitrate data for two stations in the Florida Straits reported by Riley (1939, p. 161) are summarized in table 3.

TABLE 3.—*Vertical distribution of nitrate–nitrogen (μg-atoms/L) in the Florida Straits*

Location	Station depth (meters)	Date	Levels below surface at which samples were taken (in meters)			
			1	100	200	300
Midway between Havana and Key West, Station No. 3491	1,719	May 15, 1939	1.70	0.31	0.93	14.3
Off Matanzas, Cuba, Station No. 3486	722	May 11, 1939	1.00	.50	2.21	------

Riley, Stommel, and Bumpus (1949, p. 16, fig. 6) used these surface values for southeastern Gulf water in their summary chart and discussed the origin of Caribbean water from the nutrient-poor Equatorial and Antilles Currents. They explained, however, that the Caribbean "also receives a substantial draught of Antarctic intermediate water, which is very rich, particularly in nitrate. The maximum concentration of this substance at a depth of about 800 meters in the Caribbean (and possibly the Gulf of Mexico) exceeds the amount found anywhere else in the western North Atlantic." Some of this may be accumulated products of regeneration, as suggested for phosphate (Riley 1951).

[7] There appears to be a confusion of units for expressing these nitrate data parallel to that discussed for phosphate in footnote 5.

NITRITE–NITROGEN

Distribution of nitrite–nitrogen in the Gulf of Mexico is almost unknown except for a single station in the Yucatán Channel and a few analyses of surface water along the Florida west coast made in 1946–47 by Williams (1947) and Gunter, Williams, Davis, and Smith (1948), (table 4).

TABLE 4.—*Nitrite–nitrogen along Gulf coast of Florida, 1946–47*

[Observations by Williams, Gunter, Davis, and Smith]

Area	Location	Date	Nitrite–nitrogen μg-atoms/L
Tampa Bay	Green Key, Hillsborough Bay.	Jan. 30, 1946	0
Do	do	June 4, 1946	0
Do	1 mile west of Green Key, Hillsboro Bay.	do	0
Do	Terra Ceia Bay	Jan. 29, 1946	0
Do	Terra Ceia Bay (center)	June 3, 1946	.1
Do	Terra Ceia Bay (north side)	do	.1
Cape Sable	¼ mile southwest of Catfish Key, Florida Bay.	Mar. 9, 1946	2
Do	Conchie Channel, Florida Bay.	do	.2
Do	East River, east of Whitewater Bay.	May 6, 1946	0
Key West	2½ miles north of Content Keys.	Apr. 12, 1947	0
Do	2 miles north of Barracuda Keys.	do	0

Vertical distribution of nitrite at *Atlantis* station 1606 in the middle of the Yucatán Channel May 4, 1933, depth 1,911 m., reported in the Bulletin Hydrographique (1936, p. 103) and by Rakestraw (1936, p. 149, table 9)[8] is summarized in table 5.

TABLE 5.—*Nitrite-nitrogen in the Yucatán Channel*

Depth (meters)	Nitrite-nitrogen μg-atoms/L	Depth (meters)	Nitrite-nitrogen μg-atoms/L
0	0.135	300	0.02
25	.01	400	.01
50	.01	500	.01
100	.11	600	.01
150	.035	800	.01
200	.03		

HYDROGEN ION CONCENTRATION (pH)

The hydrogen ion concentration of sea water at the Dry Tortugas from the surface to 35 meters varied between the pH values of 8.1 and 8.28 (McClendon, 1916a, 1916b, 1918; Mayor, 1922). Published data on vertical distribution of pH in deeper waters of the Gulf are limited to those taken at *Atlantis* station 1606 in the middle of the Yucatán Channel May 4, 1933. They were reported in the Bulletin Hydrographique (1936, p. 103), corrected for depth to represent conditions *in situ*, and diagrammed by Rakestraw and Smith (1937, figs. 7, 18–20). The pH increased slightly from 8.14 at the surface to 8.17 at 24 meters, then decreased to a minimum of about 7.9 at 736 meters, then increased to about 8.03 at 1,537 meters.

Measurements of the pH of shallow waters of Galveston Bay were made by Wise, Winston, and Culli (1945). Detailed studies of pH distribution at 26 stations in the coastal bays between New Orleans and Biloxi were reported by Gunter (1950); the pH values ranged from 6.66 in Pearl River entering Lake Borgne, to 8.35 in American Bay, off Breton Sound.

Determinations of pH on the sea water collected during and after the red tide (Galtsoff, 1948, pp. 23–24; Gunter, Williams, Davis, and Smith, 1948, p. 319, table 9) indicated no abnormal hydrogen ion concentrations.

ALKALINITY AND CARBON DIOXIDE

The alkalinity or buffer capacity and concentrations of carbonic acid (including the free carbon dioxide), bicarbonate, and carbonate have been studied in Gulf of Mexico water in the Dry Tortugas by Dole (1914), McClendon (1918), Mayor (1922), Wells (1922), and Lipman (1929), and in the Yucatán Channel by Mitchell and Rakestraw (1933), and Rakestraw and Smith (1937, p. 2, table 1; p. 9, fig. 7).

COPPER

According to Riley (1937) soluble copper and copper adsorbed on plankton and detritus is distributed horizontally and vertically in all directions from the mouth of the Mississippi River as far as the 1,000-fathom line. All samples analyzed by him showed the concentrations of soluble copper from 1 to 25 mg/m ^{3} and that of adsorbed copper from 0.3 to 7.2 mg/m.^{3} The high copper values in the surface samples were generally found in waters of low salinity. At the 1,000-fathom station, soluble copper increased from 5 mg/m ^{3} at the surface to 9, 10, 10, and 12 mg/m ^{3} at 100, 300, 600, and 1,800 meters depth, respectively.

MISCELLANEOUS CHEMICAL CONSTITUENTS

Bromine content of the Gulf of Mexico water has been studied in connection with the commercial

[8] The graph of this nitrite distribution (Rakestraw, 1936, p. 160, fig. 11) does not correspond to the figures in the tables.

extraction of this material at the plant constructed in 1940 at Freeport, Texas.

Calcium ranging from 427 to 535 mg/kg was reported by Lipman (1929) in two samples collected at the Dry Tortugas in July 1922. Calcium carbonate precipitation in the water in the Marquesas lagoon when the pH was 8.46 was observed by McClendon (1928, p. 258). The mechanism of this process was studied by various chemists and bacteriologists at the Dry Tortugas and elsewhere (McClendon 1918, pp. 252–258; Gee 1934; Gee and Feltham 1934).

Hydrogen sulfide was indicated in West Galveston Bay by blackening of the white lead paint on boats at a time of animal mortality (Gunter 1942). Tests for hydrogen sulfide were made on the red tide water, but no clearly positive results were found (Gunter, Williams, Davis, and Smith, 1938, p. 320).

Iron ranging from 0.12 to 1.50 mg/kg was reported by Lipman (1929) in two samples from the Dry Tortugas.

Magnesium content of 1,300 mg/kg was reported by Shigley in this book in the Gulf water at Freeport, Texas, where plants were erected for the commercial extraction of this metal from sea water.[9]

Various organic compounds have been reported present in Gulf waters. Gunter (1942) concluded that the mortality of marine organisms in an inshore area was caused by oxygen deficiency associated with decay of organic materials and the accumulation of toxic products of anaerobic decomposition. Riley (1937) reported from 0.23 to 20.60 mg/L of organic matter in the Gulf water in the area near the mouth of the Mississippi River. Both plankton and organic detritus adsorbed significant amounts of copper. Woodcock (1948) studied an unidentified human respiratory irritant, probably a product of the blooming *Gymnodinium brevis* which was carried ashore in minute droplets of sea water. A carbohydrate which showed some of the chemical properties of arabinose was found in concentrations from 2 to 25 mg/L in the natural sea water supply at the U. S. Fisheries Station at Pensacola, Florida (Collier, Ray, and Magnitzky, 1950).

Products of industrial and sewage pollution have been reported in Texas coastal waters (Burr 1945a, b; Wise, Winston, and Culli, 1945).

[9] The extraction of bromine and magnesium from sea water is discussed in an article by C. M. Shigley, The Recovery of Minerals from Sea Water, p. 153.

Potassium concentrations of 404 and 435 mg/kg were reported in two samples of sea water from the Dry Tortugas (Lipman 1929).

Silicon concentrations of 9.80 and 11.10 mg. SiO_2 per kilogram were reported in the same samples (Lipman 1929).

Solids reported by Lipman (1929) from analyses of the two samples of Dry Tortugas water are summarized in table 6.

TABLE 6.—*Solids, mg/kg, in Dry Tortugas sea water*

	Sample No. 1	Sample No. 6
Total solids	35891	37750
Nonvolatile solids	34018	34580
Volatile solids	1873	3170

Distribution of dissolved solids was studied at 26 stations in the coastal bays from New Orleans to Biloxi by Gunter (1950) who reported values ranging from 92 to 29,164 parts per million or milligrams per kilogram.

SUMMARY

Salinity distribution in the Gulf of Mexico is fairly well known except for the general absence of data on seasonal variations in offshore waters.[10] The same could be said of oxygen distribution. Phosphorus distribution is known only for four small areas: Florida Straits, Yucatán Channel, central west coast of Florida, and the Mississippi Delta region. Nitrate, nitrite, pH, alkalinity, carbon dioxide distributions are known only in the Yucatán Channel-Florida Straits corner of the Gulf and there for only one or two seasons of the year. Other chemical data are scarce, scattered, or absent.

It is expected that considerable information will soon become available with the publication of results of studies sponsored by the chemical and oil companies and of those being conducted by the research vessels and in the shore laboratories of the Fish and Wildlife Service.

[10] Seasonal and local variations of chlorinity and salinity in offshore waters of a portion of the Gulf of Mexico are being studied by the American Petroleum Institute (Project 51) through Scripps Institution of Oceanography of the University of California and the Department of Oceanography of the Agricultural and Mechanical College of Texas. Salinity data can be found in the Progress Reports of the Department of Oceanography, Agricultural and Mechanical College of Texas, Project 34, for October 1 to December 31, 1951, and January 1 to March 31, 1952.

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THE RECOVERY OF MINERALS FROM SEA WATER

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Man's hope to develop power from the sea has not yet been realized, but the prospect of recovery of minerals from that mighty storehouse has long since become real. It is the purpose of this writing to trace the history of the extraction of minerals from the seas, to describe recent large commercial projects for recovering elemental bromine and magnesium from sea water, and to briefly discuss a few of the economic factors in such sea water extraction operations.

The total volume of the oceans is estimated to be 320 million cubic miles (Armstrong and Miall, 1946). Although the salinities of the several seas vary somewhat, the average is approximately 35,000 parts of dissolved salts per million, equivalent to 165 million short tons per cubic mile. The oceans of the world thus represent a storehouse of about 50 million billion tons of dissolved materials. The chloride ion represents 54.8 percent of the total salts, the sodium ion 30.4 percent, sulphate 7.5 percent, magnesium 3.7 percent, calcium 1.2 percent, potassium 1.1 percent, carbonate 0.3 percent, and bromide 0.2 percent. Although the sea is believed to contain at least traces of every element, these eight ions account for over 99 percent of the sea water salts; all other elements total less than 1 percent.

Since the sodium and chloride ions represent six-sevenths of the dissolved salts and are the most easily extracted, it is not surprising that they seem to have been involved in the first recovery on record. Sodium chloride, common salt, was undoubtedly the first compound to be removed from sea water and used by man. It is believed that salt was used by cave men at least 5,000 years ago. Salt from sea water is mentioned in Chinese writings about 2200 B. C. Aristotle in his *Meteorologica* wrote of the origin and usefulness of the salts of sea water and described a method of "unsalting" sea water. The ancient Greeks, Romans, and Egyptians were familiar with production of salt by solar evaporation of sea water. Such salt recovery has been common in China, India, and Japan for many centuries, and still continues. Salt from sea water was produced on the Atlantic coast of North America about 1680 and on the Pacific coast in 1852. The Atlantic coast industry was short lived, but that on the Pacific coast has thrived to this time.

The production of crude soda and potash from the ashes of seaweeds was accomplished in Scotland as early as 1720. Iodine was recovered from seaweeds for the first time early in the nineteenth century; magnesia was first prepared on the Mediterranean coast at the end of the century. The records do not indicate any additional progress until 1923 when magnesium chloride and gypsum were produced from the bitterns from solar evaporation of the sea water of San Francisco Bay (Seaton 1931).

These bitterns were first treated with calcium chloride, precipitating the sea water sulfate as calcium sulfate, which was settled and filtered. Concentration of the filtrate, cooling and separation of the residual magnesium sulfate, potash, and other salts by settling and centrifuging, gave a fairly pure magnesium chloride solution which was further concentrated to salable form by boiling. The calcium sulfate resulting from the calcium chloride treatment was washed, dried, and sold as gypsum.

In 1926, the first sea water bromine was recovered on a small commercial scale by chlorinating the San Francisco Bay bitterns, steam stripping, condensing, and purifying the product.

In 1931, the production of potassium chloride by evaporation of the waters of the Dead Sea was inaugurated; in 1932, bromine was recovered on a commercial scale from the residual liquors of the potassium plant using a process similar to that employed for San Francisco bitterns.

Prior to 1933, the survival of the majority of the projects recovering material from sea water depended upon solar evaporation for initial con-

centration of the valuable sea salts. A few projects depended on adsorption or biochemical concentration as exemplified by the production of soda, potash, and iodine from seaweeds. Of the other likely methods of recovery, precipitation by a specific reagent had been demonstrated in the commercial production of magnesia by liming sea water and in the experimental removal of bromine as the insoluble tribromoaniline. The latter process was developed in 1924 by the Ethyl Gasoline Corporation and carried to large scale experimental work in the floating chemical laboratory, the S. S. *Ethyl* (Stine 1929). Separation by ion exchange processes or by selective volatilization of the material sought had not yet been commercially exploited.

In 1933, a sharp increase in the demand for ethylene dibromide as a constituent of gasoline anti-knock could not be readily met by increasing the output of bromine plants using subterranean brines. Based on experimental work done in anticipation of this need, a plant was constructed by the Ethyl-Dow Chemical Company on the Atlantic coast at Kure Beach, North Carolina, to remove bromine directly from sea water without the prior concentration which had been necessary for the earlier commercial recoveries. The significant feature of this operation was that the small amount of bromine was removed as a gas from the relatively large volume of water; past efforts had largely been directed toward removal of large amounts of water as vapor from the relatively small amounts of dissolved salts.

The original Kure Beach plant was designed to extract 6 million pounds of bromine per year for the production of ethylene dibromide. Through minor additions and process improvements the capacity was increased to nearly 9 million pounds per year. In 1937 the capacity of the plant was doubled, and in 1938, increased again, reaching an output of approximately 40 million pounds per year.

In 1940 a further increase in bromine requirements led to the erection of a plant at Freeport, Texas, to recover bromine from the waters of the Gulf of Mexico. This plant had an initial capacity of about 30 million pounds of bromine per year; a second unit of equal output was built in 1943.

Another milestone in the recovery of minerals from sea water was passed in 1941 when at Freeport, Texas, the first magnesium metal was produced from water of the Gulf of Mexico by the Dow Chemical Company. Although the precipitation of magnesium hydroxide from sea water bitterns and brines and the method of making magnesium metal from magnesium chloride were both well known prior to 1941, it was not until then that these methods were revised and integrated to give an economically feasible process for making metallic magnesium from sea water. The success of the first 18 million pounds per year magnesium plant was shown by the erection of another plant of equal size 1 year later.

In 1942, a 72 million pounds per year magnesium metal-from-sea-water plant was built by the United States Government at Velasco, Texas, as a part of the program planned to meet emergency war-time needs. The plant was designed and run by the Dow Magnesium Corporation. It operated at or above rated capacity for the duration of the war. That sea water represented no handicap as a source of raw material for the newly developed magnesium process was demonstrated by comparative costs published by the Defense Plant Corporation, after cessation of hostilities (Klagsbrunn 1945). The Velasco plant of the Dow Magnesium Corporation bettered by nearly 30 percent the lowest cost achieved by other government plants using more concentrated magnesium sources.

Unfortunately, both this government-owned magnesium project at Velasco and the privately owned bromine plant at Kure Beach were among the war casualties when wartime production capacity encountered reduced peacetime demands. However, economic survival was largely in favor of the sea-water processes. Since World War II the entire United States production of virgin magnesium and an estimated four-fifths of the bromine have been derived from sea water.

The processes which have been successfully used for bromine production at Kure Beach, North Carolina, and Freeport, Texas, and for magnesium at Freeport and Velasco, Texas, are chemically very simple. They have been described in detail in articles by Stewart (1934), Kirkpatrick (1941), Schambra (1945), and others but are worthy of brief review.

There are two bromine extraction processes. Both can achieve recoveries of bromine from sea water approaching 90 percent. The first, called the "alkaline process," is the one which was used for the initial phases of the Kure Beach develop-

ment. Sea water, which contains 69 parts per million bromine, is carefully screened to remove debris, seaweed, and fish and is continuously pumped to the top of a "blowing out tower," a brick structure packed with wood grids. On its way to the top of the tower it receives chemical additives which convert the nonvolatile bromide of the water to relatively volatile free bromine. The first additive is dilute sulphuric acid which is automatically controlled to reduce the pH of the sea water from 7.8 to 3.5 and thus suppress the hydrolysis of the free halides. The second additive is chlorine gas. This is injected in an amount slightly in excess of the equivalent bromide, converting it to free bromine. At the top of the blowing out tower the treated brine is distributed evenly over the upper layers of wood packing and trickles downward through the packing to outlet ports about 40 feet below. As it slowly moves down, a current of air is drawn into the bottom of the tower by fans at the end of the system; it passes up through openings in the grids and blows the free bromine out of the treated sea water. The latter now passes back to the ocean at some distance from the intake, little changed except for its bromine content.

The bromine-laden air from the top of the blowing out tower next passes to the soda ash absorption tower. This consists of nine spray chambers in series, each chamber having its own separate recycle system for spraying alkaline absorption liquor. Here nozzles at the top of each chamber spray a dilute soda ash solution into the air stream. The sodium carbonate reacts with the bromine and puts it into solution as a mixture of sodium bromide and sodium bromate. Continued recirculation of the alkaline solution builds up the concentration of bromide-bromate, and at regular intervals the solution of highest concentration from the chamber adjacent to the blowing out tower is pumped to a storage tank. The charges of partially brominated alkaline solution in the other chambers are each pumped forward one step, and when the solution in the weak end of the system has been forwarded the last chamber is recharged with a fresh 5 percent soda ash solution.

By means of this batch-countercurrent recirculation a solution is obtained which is nearly eight-hundred-fold more concentrated in bromine than the original sea water.

The production of pure liquid bromine from the sodium bromide-sodium bromate solution is accomplished by a second operation. The solution, which has a slight residual alkalinity, is pumped over a brick-lined scrubber tower where it serves to absorb bromine from the condenser vents. A small amount of steam is added to the bottom of the tower to preheat the liquor for the stripping step. A controlled excess of 60° Be sulphuric acid is then mixed with the liquor, and the reaction between sodium bromide and sodium bromate in the acidic solution produces free bromine. The mixture passes to a continuous steam-stripping column of acidproof construction. The bromine is distilled off and together with excess steam is liquefied in ceramic or glass condensers. The immiscible water layer saturated with bromine is returned to the stripping column. The bromine is purified by distillation, yielding elemental liquid bromine having a purity of 99.7 percent plus. The slightly acid stripping column effluent is added to the incoming sea water to utilize its relatively small acid content.

The second bromine process, known as the "acid process" or "SO_2 process," was developed in 1937 and has been used in all bromine-from-sea-water plants built in the United States since that date. In this method the acidification, chlorination, and blowing out of the sea water are carried out essentially the same as before. Into the bromine-laden air from the blowing out tower is injected a carefully controlled flow of dilute SO_2 gas prepared by burning sulphur in a conventional type burner and cooling the 10–12 percent SO_2 so obtained. The two gas streams are thoroughly mixed by passing through a system of carefully designed baffles, whereupon the bromine reacts with the slight excess of SO_2 in the presence of water vapor to give a mixture of hydrobromic and sulphuric acids in the form of a fine acid mist. The acids are readily scrubbed from the air stream by fresh water in an absorption tower. The resultant acid solution has a bromide content of approximately 7 percent, or 70,000 parts per million. This step thus accomplishes a one-thousandfold concentration of the original bromine of the sea water.

The bromine is removed from the strong acid solution by a method very similar to that employed in the "alkaline process." The acid liquor is pumped over a packed column where it

scrubs bromine from the condenser vents. It is preheated in that tower by the addition of live steam. Chlorine equivalent to three-fourths of the hydrobromic acid is added with the steam. The liquid mixture then passes to a steam stripping column where the remainder of the equivalent chlorine is added and the free bromine is steam distilled out of the solution. The bromine-steam vapor from the top of the tower is condensed as before, and purification of the liquid bromine so obtained yields a product of quality equal to that of the first described method.

The hot effluent from the stripping column consists of a mixture of hydrochloric and sulphuric acids. It is added to the incoming sea water and under normal conditions supplies approximately two-thirds of the acid requirements of the blowing-out step.

The factors which determine the competitive position of either or both of these sea water extraction processes differ only slightly from those encountered in the consideration of any economic enterprise. One must principally consider location of raw materials, efficiency of the process, materials of construction, and manpower.

The proper location of a plant utilizing either bromine process is particularly important to the success of the project. A place is required where sea water of high and constant salinity is conveniently available, free from organic contamination, and undiluted by major fresh-water rivers. It must also possess favorable circumstances for disposing of the large quantities of processed water without mixing with the unprocessed water. Where shallow water and variable currents prevail, the intake and effluent systems should be widely separated. Deep water along shore and constantly favorable shore currents lessen the need for such separation. A plant site only slightly above sea level is preferable to reduce pumping costs.

Since both processes depend on vaporization of bromine, and since the vapor pressure of bromine in sea water varies considerably with temperature, a location in a warm climate is highly desirable. Other things being equal, a blowing-out tower handling 25° C. sea water can operate at a higher rate and can produce approximately twice the amount of bromine as the same tower operating at 10° C. The absorption of the alkali process is also susceptible to temperature effects. Absorber losses are five- to fifteen-fold more at 10° C. than at 25° C., depending on the excess alkalinity of the absorbing solution. A location as near as possible to the source of economical raw materials and power and to the point of disposal of the finished product is desirable; but other factors are of secondary importance when compared with the need for favorable oceanographic and climatic conditions.

Because of the relatively large quantities of raw materials which must be handled in order to obtain each pound of bromine, it is necessary that very close operational control be maintained at all points. Since reliable indicators and automatic controls have made a large contribution to the success of the large scale recovery of bromine from sea water (Hart 1947), they must be regarded as integral parts of both processes.

The manufacture of magnesium from sea water is quite different from bromine processes. Magnesium is taken out of the sea water in an alkaline condition instead of acid and is removed by precipitation rather than blowing out.

The process is carried out in 10 well-defined steps. In the first step, sea water containing 1,300 parts per million magnesium is screened as in the bromine process and is continuously treated with an excess of milk of lime. The lime used in the present operation is prepared by calcining oyster shells at 1,200° to 1,400° C. to produce chemical lime of purity over 96 percent, slaking the lime hot, and settling the calcium hydroxide to a heavy slurry. An excess of 20 percent of the theoretical lime is necessary to keep boron compounds in solution.

The boron of the sea water, if absorbed by the hydroxide and carried through the process, gives difficulty in the final electrolysis step. The limed sea water is delivered to standard Dorr settling tanks. There the precipitated magnesium hydroxide settles to the bottom and is drawn off as a thin slurry having a composition of about 12 percent magnesium hydroxide by weight. The overflow from the Dorr tanks is discarded; it represents nearly 98 percent of the water and other materials with which the magnesium was originally associated.

The next step consists of filtering the slurry on Moore batch-type leaf filters. In this step approximately half of the remaining water and soluble materials are separated from the magnesium

hydroxide. Filter cake containing 25 percent of magnesium hydroxide by weight is obtained.

The third step provides for neutralization of the alkaline filter cake. The cake is mixed with previously prepared magnesium chloride solution and agitated to make a slurry which can be pumped. It is transferred to a neutralizing tank where an automatically controlled stream of hydrochloric acid is added to exactly neutralize the magnesium hydroxide. Thus, a 15 percent magnesium chloride solution is obtained.

The fourth step consists of evaporation of the magnesium chloride solution to eliminate water and to reduce the solubility of salts picked up from the sea water. Evaporation is accomplished in either of two ways. In the earliest or direct fired method the magnesium chloride solution is sprayed into gas fired chambers. The more recent submerged combustion method accomplishes evaporation by burning a carburated mixture of natural gas and air below the surface of a pool of magnesium chloride solution. In either case, direct contact with the hot products of combustion concentrates the solution to 35 percent magnesium chloride by weight. Direct heating is necessary because of the scaling tendency of the solution.

In the fifth step the unwanted calcium is precipitated from the solution by the closely controlled addition of magnesium sulfate. The treated liquor is held for 24 hours in an agitated tank to encourage crystal growth of the salt and gypsum.

The adjusted evaporator product is then filtered, first through Moore filters identical to those used earlier for the magnesium hydroxide filtration, and then through plate and frame presses for a final polish.

The seventh step of the process is evaporation of the filtered 35 percent magnesium chloride solution to a concentration of approximately 50 percent. Open top, brick-lined steel boiling kettles heated by alloy steam coils are used for this purpose.

In the next stage, the concentrated magnesium chloride liquor at a temperature of 170° C. is transformed into a solid suitable for feeding the electrolytic cells. The hot liquid is sprayed on 6 to 10 times its weight of previously dried solid in a horizontal rotary mixer, producing a white granular material containing about 68 percent magnesium chloride. This is dried with hot recirculated air in a multi-shelf drier, similar in design to a Herreshoff furnace, and becomes a free-flowing granular cell feed of approximate composition $MgCl_2.1.5H_2O$. Part of the dry granular material is returned to the rotary mixer and part is conveyed to the magnesium cells.

The ninth step is electrolysis of the cell feed (Hunter 1944). The electrolytic cells used for this operation are bathtub shaped steel pots of approximately 2,500 gallons capacity, filled with a fused salt mixture consisting of 25 percent $MgCl_2$, 15 percent $CaCl_2$, and 60 percent NaCl at 700° C. Graphite electrodes suspended in the bath serve as anodes; the pots and their internal baffles act as cathodes. Passage of a high amperage, direct current between the electrodes and the pot decomposes the magnesium chloride of the bath to elemental magnesium and chlorine gas. Cell feed is added continuously to maintain the proper bath composition and level. The hot gaseous products are collected under a tightly fitting refractory cell cover, cooled, and piped to the hydrochloric acid plant. The molten magnesium metal rises to the top of the bath where it is trapped by inverted troughs and conveyed to the storage wells in the front of each cell.

The metal is hand dipped from the cells three times daily and cast into the familiar 18-pound notched ingots. Each cell, operating at 60,000 amperes, produces approximately 1,200 pounds of magnesium per day having a purity in excess of 99.8 percent. No other refinement is necessary to meet the specifications for commercially pure magnesium.

The final step of the process consists of converting the chlorine from the cells to hydrogen chloride by high temperature reaction with steam and natural gas in a regenerative furnace. A small amount of unreacted chlorine is reduced by the controlled addition of SO_2 supplied by conventional sulphur burners. The hydrogen chloride and the small amount of H_2SO_4 are absorbed in water, and the resulting acid solution is recycled to the neutralizers for the reaction with $Mg(OH)_2$ previously mentioned.

Since process losses are inevitable, it is necessary to replenish the recycled hydrochloric acid to the extent of about one-half pound per pound of magnesium produced. This may be added as chlorine

to the gas stream entering the furnace or as hydrochloric acid at the neutralizers.

The properties and uses of magnesium are well-known but warrant brief comment. It is the lightest structural metal commercially available. It is about one-fourth as heavy as iron and two-thirds as heavy as aluminum. When alloyed with small amounts of other metals, such as aluminum, zinc, and manganese, it has a high strength to weight ratio, it is easily fabricated, and it has good corrosion resistance. These properties make it advantageous for use in light weight structures and equipment such as airplanes, truck and trailer bodies, portable tools, hand trucks, ladders, and others too numerous to mention. The high place held by magnesium in the electromotive series of metals makes it outstanding for sacrificial anodes—in other words, sources of current for the protection of buried or submerged metal surfaces against corrosion. One of the more recently developed uses of magnesium is in the field of ferrous metallurgy. Small amounts of magnesium properly added to cast iron prior to pouring give a so-called "nodular cast iron" which has strength and ductility properties similar to those of steel.

The economic factors involved in the magnesium-from-sea-water operation are somewhat different from those of bromine. From an oceanographic or climatic standpoint, the location is not so critical. The sea water which must be processed per pound of magnesium is only one-twentieth as much as is required per pound of bromine. The water temperature has little effect on the magnesium recovery. More important is a location favorable to the supply of raw materials and power. The convenient availability of lime and abundant and inexpensive fuel and power are obviously essential for competitive operation.

The process can achieve a recovery of 85 to 90 percent of the magnesium in sea water. The performance of each step represents a compromise between high efficiency and high capital cost, and the justifiable recovery must be calculated for the conditions of each plant. The process has the inherent advantage that the majority of the materials can be conveyed by pumping. Most of the steps are continuous and subject to the benefits of automatic control.

The quantities of sea water and oyster shells used in the process are large. In the Freeport plant (following quoted from Schambra, 1945, pp. 4, 6):

"Sea water flows by tidal surge from deep water in the Gulf of Mexico, through the 40 ft. deep channel dredged into the Freeport harbor. Stone jetties at the mouth of the harbor prevent the surf and shore currents from washing sand into the channel. One mile inshore from the harbor mouth, the plant intake withdraws the raw sea water at a depth of 25 ft. A concrete curtain wall holds back the surface water so that the suction opening is actually between −20.0 ft. and −30.0 ft. elevation. In waters of this locality, stratification of high and low density water occurs, even in the range of specific gravity of 1.000 to 1.026, the difference between fresh water and full strength sea water. The use of a curtain wall permits withdrawal of 80% to 90% full strength sea water when the surface may be nearly fresh water. Due to rains and fresh water intrusion from the Brazos River, the sea water at the intake averages 85% of full strength.

At the intake, trash, marine plants, and small fish are removed by a triple screening . . . Four Worthington submerged-propeller axial-flow type pumps, each delivering 70,000 g. p. m., raise the sea water from a varying sea level to a constant head at elevation 9.0 ft. Each pump discharges directly into a unique rotating barrel [Monel] screen . . . made up in wood-framed trays which are bolted to the steel barrel framework. Each tray is carefully insulated from the barrel by rubber gaskets to minimize bi-metal electrolytic corrosion.

Following the screens, the sea water is chlorinated continuously to a residual of 0.2 to 0.5 p. p. m. free halogen. Growth of marine plants, barnacles, and oysters is prevented in this manner . . . Shell [used for the production of lime] is purchased from two dredging companies now working the oyster shell reefs in Galveston bay. Accumulated shells of dead oysters lie in irregular reefs in 1 to 17 ft. of water, with the thickness of the beds varying from 1 to 30 ft. There are millions of tons of usable shell in Galveston and Matagorda Bays alone. Extensive reefs are found off shore in the Gulf. Newly dredged shell contains mud and sand which are removed by washing on the dredge with sea water. The dredge *W. D. Haden* has a capacity of 350 tons per hr. of washed shell. Loaded barges of 800 tons capacity are removed by Diesel tug to the Freeport plant . . . The washed shell is fed either to the storage pile or directly to the kiln feed hoppers . . . Each kiln produces 150 tons of lime per day.[1]

In conclusion, the large-scale recoveries of bromine and magnesium from sea water must not be regarded as merely incidents in the record of scientific progress of the last three decades. They are indicative of a pronounced trend toward using the seas for more of life's needs.

It is natural that this should be so. The seas, covering three-fourths of the earth's surface and

[1] Reproduced with the permission of the American Institute of Chemical Engineers from the Transactions of the A. I. Ch. E., vol. 41, No. 1, pp. 4, 6.

bordering upon every continent, represent a global source of supply. They are practically inexhaustible, for the total quantities of available salts reach astronomical figures and are unquestionably increasing with the daily contribution of the rivers, while other mineral resources are being depleted. The handling of sea water by pumping is unquestionably easier and cheaper than the majority of mining methods. The sea water has relatively stable chemical and physical properties, contributing to constancy of the finished product.

All these things, and more, lead to the inevitable conclusion that the record of past achievements and the vision of man's increasing dependency on the oceans will combine to stimulate the research activities of all the nations toward a more complete utilization of the tremendous resources of the seas.

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CHAPTER V

PLANT AND ANIMAL COMMUNITIES

PHYTOPLANKTON OF THE GULF OF MEXICO

By CHARLES C. DAVIS, *Western Reserve University*

As late as 1944 Dr. B. F. Osorio Tafall, writing concerning the interesting distribution of *Biddulphia sinensis* Greville, found it necessary to speak of "La carenzia absoluta de estudios sistemáticos del plancton en años anteriores en las aguas del Caribe y del Golfo de México . . ." It is true still that little has been done on taxonomic studies of Gulf of Mexico phytoplankters, and even fewer ecological studies have been made.

The earliest published observations on the phytoplankton of the Gulf of Mexico appear to be those of Alexander Agassiz (1888) who mentioned, in very general terms, the occurrence of Coccolithophoridae in the central regions of the Gulf. He mentioned more specifically the occurrence of large chains and patches "of dirty yellow color" of the filamentous blue-green alga he identified as "probably" the same as the *Trichodesmium erythraeum* that is so famous in the Red Sea. Dr. Drouet of the Chicago Natural History Museum has identified the most common filamentous blue-green alga from Florida and Texas marine waters as *Skujaella* [*Trichodesmium*] *thiebauti* (Davis, 1950), and probably this is the species referred to above. Agassiz also referred to the occurrence everywhere, but in small patches only, of a species of *Sargassum*.

From the time of Agassiz' (op. cit.) early superficial report until 1937 there were no detailed reports on Gulf of Mexico phytoplankters other than individual species records such as that of Taylor (1928) who listed the occurrence of *Skujaella* [*Trichodesmium*] *thiebauti* and of two common pelagic species of *Sargassum* (*S. natans* and *S. fluitans*) near or at the Tortugas Laboratory. In addition, there were certain other studies made at the Tortugas Laboratory which, however, appear not to have been reported in detail. Thus, Grave and Burkenroad (1928–29) reported diatoms among those plankters that were abundant or that occurred regularly, while Conger (1925–26, 1926–27, 1927–28, 1928–29, 1937–38, 1938–39) briefly summarized his work on diatoms, some of them planktonic. Conger (1926–27) found that the diatom flora of the Dry Tortugas was strongly local in character and that it had its nearest affinities to the West Indian flora. His (Conger 1937–38) investigations showed that there was little change of quantity or kinds of the planktonic diatoms during his 10-week (summer) stay at the laboratory except that there was "some slight increase" in abundance after a period of heavy wind. He emphasized that the region of the Dry Tortugas is a silica-poor region and that Si is a limiting factor there in diatom production. For comparative purposes he (Conger 1927–28) also studied some samples from Tampa Bay and found the water rich with plankton. He stated that the "richness of this area in diatoms may account for the abundance of marine life there."

Riley (1937, 1938) studied phytoplankton production in Gulf waters, largely through the plant pigment method. In his former report (Riley 1937) he considered the influence of the Mississippi River drainage upon the phytoplankton in the northern portion of the Gulf. A number of stations were established from Galveston to Mobile and south to the thousand-fathom line (fig. 44). Analyses were made of salinity, phosphate, copper, plant pigments, and weight of organic matter. It was found that the water of the Mississippi River itself was very rich in phosphates and that this water spread over the surface of the northern Gulf both to the east and to the west but especially to the east in the direction of Mobile (fig. 45). Plant pigments were highest in the waters richest in phosphates (fig. 46). Samples obtained from completely fresh river water contained higher values for plant pigments than elsewhere, but these values were not especially high for fresh waters. This indicated that the high turbidity of the river water was a deterrent to phytoplankton growth, for nutrient conditions were especially favorable for phytoplankton production. Analyses in the open Gulf showed typically low values.

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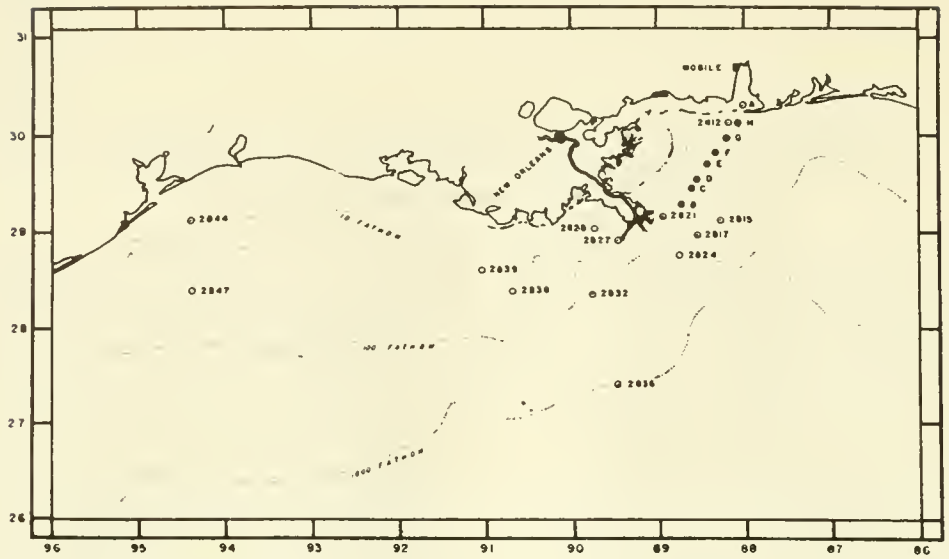

FIGURE 44.—Stations established by Riley (1937) in the northern portion of the Gulf of Mexico.

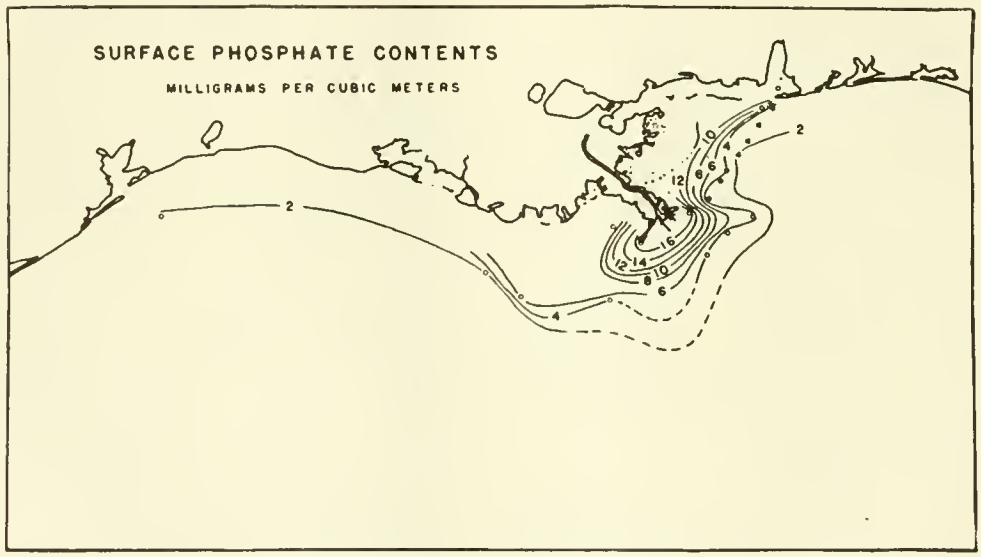

FIGURE 45.—Distribution of phosphates in the waters of the northern portion of the Gulf of Mexico.

The later work by Riley (1938) was done in the Dry Tortugas at the end of the chain of the Florida Keys in the eastern part of the Gulf. Here the water was shallow and with no influence of land drainage of any consequence. Some samples were taken at the edge of the Gulf Stream, but most of them were taken at two regular stations between Loggerhead Key and Garden Key. Plankton samples were obtained by sieving 400 liters of water through a No. 20 silk net, and a second set of samples was obtained by filtering from 3 to 10 liters through a Whatman No. 2 filter paper. Part of each net sample was studied for number of animals present, for plankton weight, and for organic material weight, while the remainder was studied for the quantity of plant pigments. It was found that the plant pigments of the net plankton constituted less than 2 percent of that occurring in the filtered samples. Thus, the mean value for the net plankton was 17 Harvey units per $m.^3$, while the average for the total plankton was 924 Harvey units per $m.^3$, indicating a very high proportion of nannoplankton. The total quantity of plankton

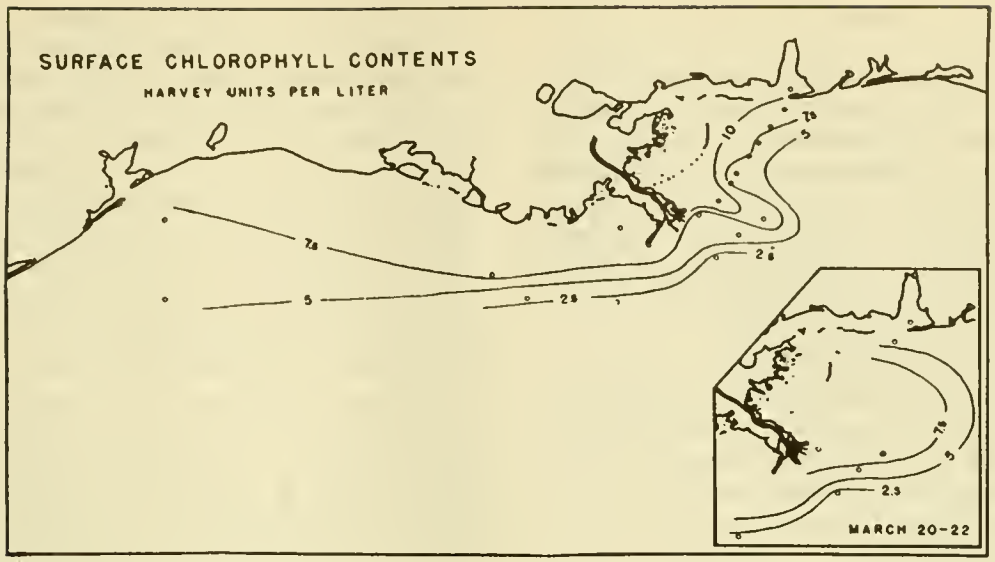

FIGURE 46.—Distribution of plant pigments in the waters of the northern portion of the Gulf of Mexico.

was much less than that to be found in most higher latitudes, the net plankton being approximately 1 percent of the spring bloom conditions in the English Channel. The total chlorophyll at the station that lay closest to Loggerhead Key (it was the less productive of Riley's two main stations) was only about 4 percent of the summer crop determined by the same author in Long Island Sound by similar methods.

Riley (1938) also attempted to study productivity and limiting factors in productivity by means of oxygen determinations in sea water samples that had been confined in white and dark bottles. To some of these, nitrates and phosphates had been added. He found that in the waters of the Tortugas region the nitrates were more important than the phosphates as limiting factors in phytoplankton production.

Parr (1939) made a quantitative study of pelagic species of *Sargassum* in the western North Atlantic, the Caribbean Sea, Cayman Sea, and the Gulf of Mexico. Samples were obtained by dragging a special net at the surface of the water while the *Atlantis* was traveling from station to station on hydrographic cruises. For each sample, the catch was sorted as to species and weighed on board ship. Within the Gulf of Mexico proper, a total of 26 samples was obtained during the spring months (February 16 to April 12) of 1935. To obtain these samples, the net was dragged through the water for 1,230.5 miles. *Sargassum* was not uniformly distributed in the Gulf. The outer portions of the Gulf had a very sparse population of the weed, whereas, the concentration in the inner portion was second only to that of the Sargasso Sea itself. Parr (op. cit.) calculated that within the region of abundance, which he thought to occupy about 90,000 square miles, the crop of *Sargassum* amounted to approximately 1 ton per square mile.

The *Sargassum* crop, at the time of sampling in the Gulf of Mexico, was in very poor physical condition, the plants being small and moribund. The occurrence of the maximum in the inner portion of the Gulf, completely isolated as it was from the primary maximum in the Sargasso Sea by a wide expanse of *Sargassum*–poor water, agrees with the results of hydrographic work published by Parr (1935) and reported on elsewhere in this book, to the effect that there appears to be no great volume of surface water floating from the Gulf of Mexico to Florida Strait during the period of examination. The nearly complete isolation of the Gulf maximum from the maximum of the Sargasso Sea is also emphasized by the fact that the epizoan fauna in the two regions is very different. From his observations, Parr (1939) believes, however, that the Gulf community is not a self-sustaining community in the same way that the Sargasso Sea community is. He based this belief on the com-

paratively poor quality of the plants in the Gulf.

In his investigation, Parr (1939) found that the taxonomy of *Sargassum* is very confused and that there are many variations which, however, merge into one another. He found that in the Gulf the form he designated as *S. natans* (I) composed 87 percent of the specimens with approximately 6.5 percent each for *S. natans* (VIII) and *S. fluitans* (III). Small quantities of *S. natans* (II) and *S. fluitans* (X) were also observed.

The next paper to appear on the phytoplankton of the Gulf was written by Osorio Tafall (1944) who dealt, however, only with a single species, namely, with the diatom, *Biddulphia sinensis* Greville. He found this species in samples obtained near Tampico, Tamaulipas, Mexico. The species has an interesting distribution in the oceans of the world, but on the Atlantic Coast of the New World it had previously been described only from off the coast of South America. Osorio Tafall discussed the manner in which *B. sinensis* may have reached the waters of the Gulf of Mexico but was unable to come to any definite conclusions because of a lack of previous investigations of the phytoplankton of the Gulf. He thought it might be a relic of a previous flora, or that it might have been carried to the Tampico region from the North Sea on the hulls of boats, or that it might have been carried there by currents from its center of distribution off the east coast of South America. He favored the last-mentioned hypothesis and pointed out that if the hypothesis were correct the species would be widespread along the coasts south of Tampico, a matter easily determined by further investigation.

The disastrous "red tide" of the southwestern coast of Florida in 1946 and 1947 stimulated considerable interest in the phytoplankton of the whole Gulf. It became painfully evident that all investigations of the phytoplankton bloom that was associated with the catastrophe were greatly hampered by the lack of previous knowledge of conditions in the Gulf. Red tide is being discussed elsewhere in the present book (p. 173), and only those aspects that could not be adequately dealt with at that place will be discussed here.

Davis (1948a) mentioned cases in which *Gymnodinium brevis* Davis occurred in the plankton in very large numbers, up to 60 million cells per liter. The same author (1951) pointed out that in two of the samples under discussion this species constituted 99.28 and 98.99 percent of the total organisms present. Most of the other organisms were diatoms. Gunter et al. (1948), in addition to discussing the red tide as such, discussed other associated phenomena in the plankton cycle. Color changes of the water, as deciphered by these authors, are described in the section on the red tide. Gunter et al. (op. cit.) described in some detail other plankters, both animal and plant, associated with these changes. They summarized the sequence as follows (pp. 318–319):

> There was first the appearance of numbers of *Gymnodinium brevis* mixed in with other normal plankton types, mostly diatoms . . . Locally, or over large areas there then appeared a "bloom" of *Gymnodinium*, and in these areas the mortality occurred. This was then followed by the decomposition of many dead organisms, with the consequent release into the water of much nutrient material. Bacteria and/or phytoplankton utilized this nutrient material, and then were themselves utilized, especially by the Copepoda, which consequently increased enormously in the plankton . . . The Copepoda devoured all the suitable diatoms, and left only the species of *Rhizosolenia*, which would be very difficult for the copepods to handle . . .

Davis (1948b) described a plankton tow taken in Long Lake, a brackish-water tributary to Florida Bay. He mentioned naviculoid diatoms and *Ceratium furca* as being present but not abundant, and as being far overshadowed by large numbers of copepods.[1] Davis and Williams (1950) described a more extensive series of samples obtained from 28 lakes, bays, and sounds in the mangrove areas of southern Florida. All samples were obtained from brackish bodies of water including Florida Bay and bodies tributary to Florida Bay or directly tributary to the Gulf of Mexico. They made few identifications of phytoplankters to species. Such forms as *Rhabdonema*, *Skeletonema*, and *Ceratium* were confined to those bodies of water that were most saline, while *Coscinodiscus* was much more abundant in such localities. On the other hand, *Chaetoceros* was not so greatly limited by salt content, though it did not occur in localities with less than 3.06 parts per thousand salinity. They found that desmids were confined to the freshest bay and that green algae and blue-green algae (with the exception of *Skujaella thiebauti*) were found only in those lakes and bays with the lowest salinities. *Gonyaulax*

[1] See article on zooplankton by H. B. Moore, pp. 117–172.

spinifera (?) occurred in vast swarms in many localities on the south coast (parts of Florida Bay and some of its tributaries) and in salinities ranging from 8.60 parts per thousand in Seven Palm Lake to 25.12 parts per thousand in Upper Terrapin Bay.

In addition, Davis (1950) has dealt with phytoplankton and zooplankton from various Florida marine waters. Many of the samples analyzed were taken in the Gulf of Mexico (as far out as 60 miles west of Anclote Light) and its inland tidal waters. A large proportion of the inshore and inland-water plankters was obtained coincident to the study of the red tide, and they were reported in more detail than was possible in Gunter et al. (1948). Davis (op. cit.) stated that: ". . . the plankton appears to be richer on the west coast [than on the east coast of the peninsula], and a number of important species were confined to west coast waters." He listed, among the plants, the following that were confined to the west coast: *Baccilaria* sp., *Cerataulina* sp., *Hemiaulus* sp., *Gymnodinium brevis*, *Striatella* sp., and *Noctiluca scintillans*.

Joseph King (1950) also discussed both phytoplankters and zooplankters collected during 1949 from the west coast of Florida. He established a series of stations extending off shore to the 100-fathom line in the Fort Myers region, and these were visited several times. In addition, samples were obtained one or more times from certain other locations near the coast (fig. 47). He found that the waters in question were poor in plankton. Greatest plankton volumes were obtained at the station established over a 5-fathom depth of water. He observed a sporadic bloom of the blue-green alga, *Trichodesmium* [*Skujaella*] *erythraeum*, which at the height of growth formed yellowish flocculent windrows on the surface. He found diatoms to be numerous, especially in the inshore waters, the most abundant being *Coscinodiscus*, *Skeletonema*, *Navicula*, *Nitzschia*, *Surirella*, *Chaetoceros*, and *Rhizosolenia*. Fresh-water green algae, including desmids, were encountered at two of the stations located in estuaries. Dinoflagellates were abundant in his samples only on three occasions, all of them in inside waters (twice in Sarasota Bay and once in the estuary at Fort Myers). In each of these three cases there was a dense bloom of *Gonyaulax*, forming scattered streaks and patches of a reddish-brown film over the surface of the water. Mullet appeared to be feeding voraciously on this bloom. The species of *Gonyaulax*, or else the conditions in which it was living, may have been very different from those described by Connell and Cross (1950) in Offatts Bayou near Galveston, Texas, for in the latter case the regularly occurring red water of the bloom of *Gonyaulax* was accompanied by fish mortality and foul odors. Gunter (1951), on the other hand, believes that the occurrence of *Gonyaulax* in Offatts Bayou is only incidental to the mortality and that the mortality was directly caused by a seasonal stagnation and putrefaction accompanied by oxygen depletion. This view also had been previously expressed by Gunter (1942).

King (op. cit.) found that in the offshore waters of the open Gulf all forms of phytoplankton were very scarce. Several diatom genera were represented: the most common were *Chaetoceros*, *Rhizosolenia*, and *Thalassiothrix*, but none occurred in any abundance.

From the above it is fairly obvious that the greatest immediate need in the field of phytoplankton research in the Gulf of Mexico is a thoroughgoing quantitative study of the seasonal distribution of the phytoplankton in all portions of the Gulf. True as this statement is for the net plankton, it is far more true for the nannoplankton which has hardly been considered at all except to a limited extent in the studies of *Gymnodinium brevis* and the red tide (Davis 1948a, 1951; King 1949).

Also needed are (1) further production studies such as those attempted on a small scale by Riley (1938), (2) detailed studies of the phytoplankton-zooplankton interrelationships in the Gulf, a field practically untouched by previous investigators, (3) studies of the nutrient needs of the more abundant individual species, and (4) studies of the utilization of the Gulf phytoplankton by benthic and nektonic animals.

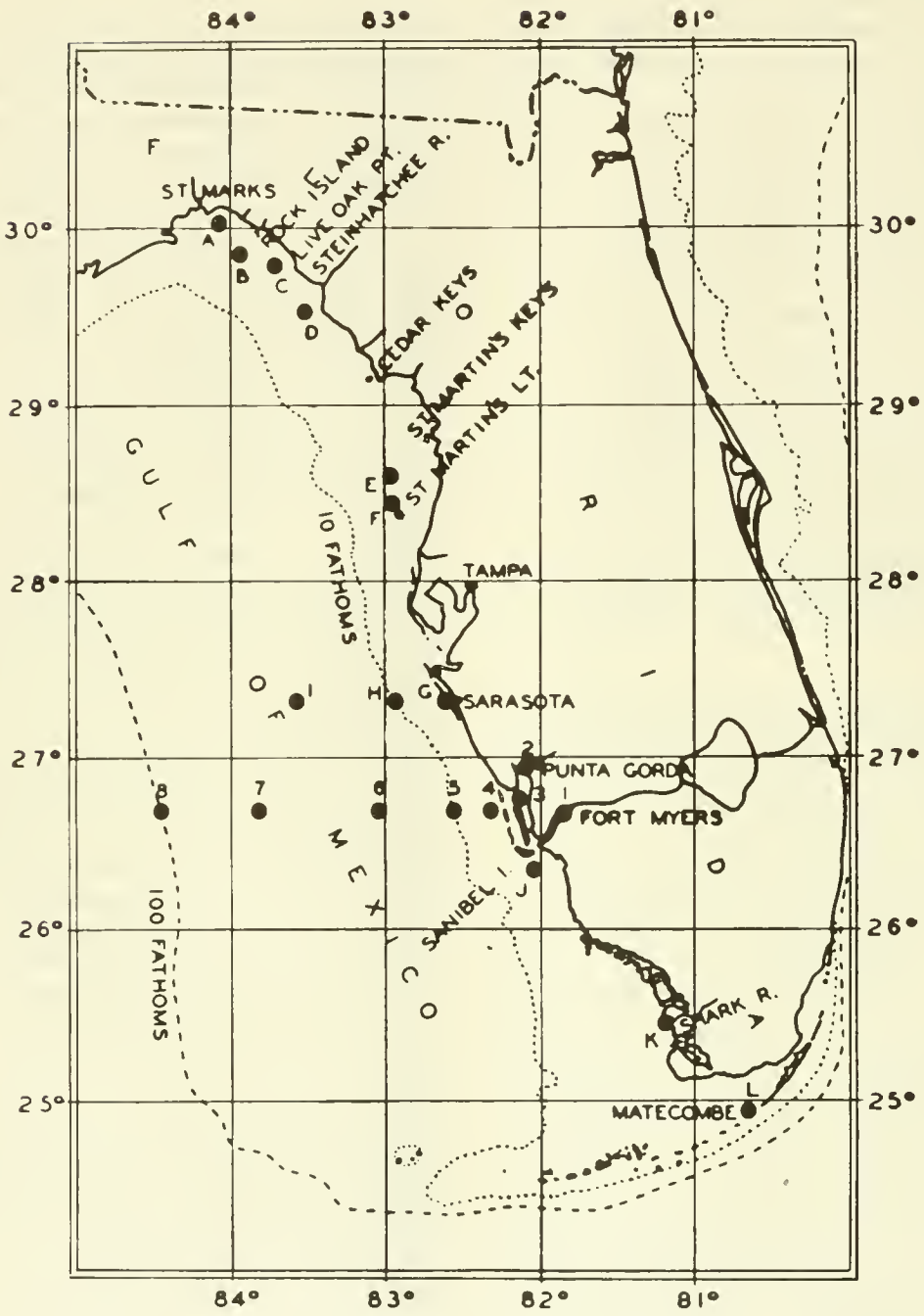

FIGURE 47.—Stations established by Joseph King in Florida west coast waters.

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THE ZOOPLANKTON OF THE GULF OF MEXICO

By HILARY B. MOORE, *Marine Laboratory, University of Miami*[1]

No major expeditions have collected zooplankton from the Gulf area. Most of the collections which have been made were from coastal waters, and none of these have been completely described. Some of the collections are still being worked on, while others could no doubt be available for study if required. No complete reference collection of the various species appears to exist.

Those published accounts of the zooplankton which have been traced are listed below. In view of their scattered nature and the fact that brief reference to material from the area may occur in papers on other areas, the list is almost certainly incomplete. A list of known collections and what could be ascertained on their present status is also included.

Burkenroad (1932) reports on nine species of euthecosomatous and one of gymnosomatous pteropods from Louisiana. Davis (1948) lists three species, one of them new, of copepods from a brackish habitat and mentions unidentified ctenophores. In another paper (1950) he gives a full account of 35 open water and 10 inshore hauls from the area. None of the hauls were from deep water. This paper also contains a survey of his own data and references to related work.

King (1950) describes the samples taken over a 10-month period in the St. Marks-Fort Myers region. Except for some copepods, few specific identifications are given.[2]

Osorio Tafall (1942) reviews previous work on Mexican rotifers and gives a detailed study of certain genera including fresh water, brackish, and marine species.

Riley's (1937) work is mainly concerned with phytoplankton–nutrient salt relations but is important in indicating an area of high standing crop off the mouth of the Mississippi. The productivity of the waters emerging from the Gulf of Mexico into the Florida current is discussed in his paper on the plankton of the Tortugas region (Riley 1938).

An ecological survey of the waters adjacent to Miami (Smith et al., 1950), although not within the area, deals with the water of primarily Gulf origin and is therefore relevant for Gulf of Mexico studies.

MATERIAL

Various plankton collections made in the Gulf of Mexico are now located in the following institutions:

Scripps Institution of Oceanography.—F. B. Phleger is working on Foraminifera from 27 series of tow-nettings taken from the surface to 2,000 meters. He states that the remainder of the material has been passed on to Yale University.

Texas Christian University.—W. G. Hewatt has a considerable amount of material which is still being worked on. In 1944–46 frequent samples were taken from Barataria Bay, Louisiana; in 1947 samples were taken from an extended area of Louisiana embayments; in 1948 samples were taken from the east side of the Mississippi Delta, Mobile Bay, and Pensacola Bay.

Texas Game and Fish Commission.—J. L. Baughman has a collection of samples from the Rockport neighborhood.

Fish and Wildlife Service, United States Department of the Interior.—P. A. Butler has a series of weekly samples for a period of about 18 months taken in Santa Rosa Sound. These are partially worked up.

United States National Museum.—Has a partly identified collection of medusae from the Gulf made by M. D. Burkenroad.

Institute of Marine Science.—Has a collection of Gulf copepods which are being worked on. To date, 11 species have been identified.

Zoological Museum of Copenhagen.—P. Heegard of the Zoological Museum of Copenhagen made collections of larval penaeid shrimp from the Gulf.

[1] Contribution No. 102 from the Marine Laboratory, University of Miami.

[2] See article on Copepoda by W. L. Schmitt, pp. 439–442.

Marine Laboratory, University of Miami.—H. B. Moore has a named collection of oceanic copepods, chaetognathes, siphonophores, and tunicates from the Florida current and Sargasso Sea. This collection is being extended to cover other groups and should prove useful in identification of Gulf material.

It is apparent from the paucity of material presented in this section that we know next to nothing of the zooplankton of the Gulf of Mexico. The importance of improving our knowledge is obvious. To mention only a few reasons: plankton forms the major fraction of the food of many fishes; it contributes largely to the food of bottom-living organisms; it contributes to bottom sediments; it can provide a valuable indicator of water movements; it may be used as an indicator of good fishing areas; and it is sometimes the cause of catastrophic mortality in fishes.

Probably the first essential step in any plankton investigation of the area must be the identification of the species present. Here a little is known from inshore waters and almost nothing from deep water. Next, or in parallel with this, a survey is needed to show the geographic distribution and relative abundance of the various species throughout the area. While the more common species call for particular study here, some of the rarer ones may prove particularly suitable for use as "indicator species." From there on, different types of investigations will call for more detailed studies of different aspects of the plankton. Fishery investigations will be concerned with the distribution and life histories of fishes and economically important invertebrates whose larvae are planktonic at some stage. It will also be concerned with the ecology of those species, probably copepods in particular, which are important as fish food. It will be concerned in the water movements in the area and so of indicator species useful in tracing these movements. Finally, it will be concerned in the details of the productivity of the various areas insofar as these bear on fish production. To the hydrographer, also, this latter aspect is of importance. To the geologist concerned with the formation of sediments the shelled forms, such as Foraminifera and pteropods and all aspects of their ecology, are of classic importance, but all organisms which contribute to the sediments are significant, and those which contribute organic matter may be of particular importance to the petroleum geologist.

It is, in fact, clear that almost all aspects of investigation of the waters of the Gulf will be directly or indirectly concerned with plankton. There are, at present, few investigators working on plankton problems of the area. More are needed, and the available supply is so small that they will probably have to be specially trained. It is to be hoped that adequately supported projects may be forthcoming to carry on at least some of the lines of work which have been suggested.

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RED TIDE

By Reuben Lasker and F. G. Walton Smith, *Marine Laboratory, University of Miami*[1]

The nature of phytoplankton blooms, i. e., the extensive production of microscopic aquatic flora in localized areas, is today, as in the past, an unsolved problem facing the biologist, oceanographer, and limnologist. Many scientific reports attribute the wholesale death of fishes and other marine organisms to these phenomena. Since the water which is affected is discolored, resulting in an amber or red color, the popular terminology has provided names for an outburst of this sort ranging from "yellow water," "rotten water," and "red plague," to the term now in common use, the "red tide."

Outbreaks of discolored water are common throughout the oceans of the world. These may or may not be associated with fish mortalities. A comprehensive record of fish mortalities due to poisoning of water by dinoflagellates and other phytoplankton is given by Bröngersma–Sanders (1948).

The Gulf of Mexico has probably been the scene of fish mortalities throughout its geological history (Bröngersma–Sanders, 1948). Written records, however, date back only to 1844. Recorded fish mortalities took place in the Gulf of Mexico in the years 1844, 1854, 1878, 1880, 1882, 1883, 1908, 1916, and 1946. In some places, such as Offatts Bayou in Galveston Bay, there is an annual recurring mortality (Connell and Cross, 1950).

The events associated with the 1844 and 1854 incidents are briefly recorded by Ingersoll (1882) in the Proceedings of the U. S. National Museum. The 1878 outburst was located near Cedar Keys and particularly off the Anclotes. Vast quantities of dead sponges were found, and the profitable sponging grounds in that area were badly depleted. In 1880 an area extending from the southern shore of Tampa Bay, from Egmont Key at its mouth, southward to Shark River and Whitewater Bay, was the scene of mass fish mortalities. Hordes of fishes and other aquatic animals were found dead and dying. Fatal patches were also found southward through Bahia Honda passage, beyond Key West, and in some places as far as the Tortugas.

Another account of "poisoned water" in the Gulf (Anonymous, 1883) cited an area off Indian Pass, approximately 1 mile long, between Clearwater and Egmont Light. The streak of "poisoned water" was covered with all varieties of dead fish. The total of individual fish deaths was not estimated.

Similar mortalities broke out in this area in 1883, 1908, and 1916. The 1916 instance was particularly severe and lasted from October 3 until the end of November of that year. Representatives of all fishes local to the area between Boca Grande and Marco were killed, although few other aquatic animals were affected. Taylor (1917) found no extraordinary numbers of dinoflagellates but observed that "the evidences contrary to such an explanation [were] not altogether convincing." His late arrival on the scene of the then current red tide may have accounted for the absence of the organisms.

In most cases, nauseating odors and the tendency for sneezing and respiratory distress were present. Discolored water was reported in all but a few accounts of mortality. It is quite plausible that the noxiousness, and particularly the discoloration of the water, was due to heavy concentrations of toxigenic phytoplanktonic organisms in practically all the cited cases.

Most of our information regarding recent outbreaks of red tide in the Gulf of Mexico stems from investigations made by several independent workers and organizations during the red tide of 1946–1947. (Gunter, 1947; Gunter et al., 1948; Davis, 1948; Ketchum and Keen, 1948; King, 1950; Smith, 1949; Woodcock, 1948.) An excellent review is offered by Galtsoff (1948, 1949).

Between November 1946 and August 1947 approximately half a million fish were annihilated. The Florida west coast fishery industry suffered

[1]Contribution No. 104 from the Marine Laboratory, University of Miami.

heavily from this loss. The area affected by this red tide extended from Sarasota southward to the Dry Tortugas. This was approximately 150 miles long and encompassed an area of several thousand square miles.

Davis (1948) identified the causative agent of the noxious water and the consequent fish deaths as *Gymnodinium brevis*, a new species of dinoflagellate. In some places the concentration of the organism was nearly 15 million cells per liter. Also, a definite sequence of discoloration took place. The initial discolored water was an "opaque" green as distinguished from the normal clear green. Following this came a yellowish green and later a greenish yellow. The water next took on a bright saffron yellow and became viscid and oily to the touch. This yellow water was associated with dying fish and was apparently caused by *G. brevis*; this organism contained individually several yellow-green chloroplasts. Other organisms were dominant at the same time and will be given consideration later. After the yellow water stage the water turned brown slowly and then "red." The "red" was actually an opaque, dull, dark amber with a greenish yellow cast. At the end of the cycle the water reverted to an opaque green and finally to its normal appearance.

Red water similar to that which appeared at the end of the discoloration cycle is believed to be caused by purple sulfur bacteria (Hayes and Austin, 1950). ZoBell (1946, p. 165) states, "Extensive populations of purple sulfur bacteria . . . growing associated with decomposing plankton including algae, jellyfish, etc., imparted a distinctly red coloration to the sea. . . . It is significant that the hydrographic conditions in 'Bloody seas' are generally precisely those which would promote the growth of purple sulfur bacteria; namely, the presence of an abundance of decomposing plankton material which provides for H_2S production and reduced oxygen tension." In the red water stage in the Gulf few *Gymnodinium* were found, since most had previously perished. Animal plankton was found to dominate at that time but did not cause the red water (Gunter et al., 1948).

The poison produced by huge numbers of *G. brevis* is a powerful toxic agent to fish. This was proved experimentally in the laboratory by placing live and healthy fishes into Florida Bay water containing dense masses of *Gymnodinium*; similar fishes were placed into a control tank containing Biscayne Bay water. Both tanks were aerated strongly by means of electric pumps. All the fishes in the test tank died, while those in the control were unaffected (Gunter et al., 1948).

Pharmacological studies have been made of a dinoflagellate-produced poison which infected shellfish off the coast of California (Sommer et al., 1948; Riegel et al., 1949), but as yet its exact chemical structure has not been described.

Connell and Cross (1950) state that a species of the dinoflagellate *Gonyaulax* produces a lethal anaerobic condition in Offatts Bayou (Galveston Bay) by its own high biochemical oxygen demand. This condition was suggested as the cause of the fish deaths that took place therein. In the red tide observations of 1946–1947 the oxygen content in the affected waters, as a rule, was normal.

It is evident that one or several genera of dinoflagellates are the causative agents of death-producing blooms of phytoplankton. These organisms, studied by both botanists and zoologists, exhibit a wide range of morphological and physiological differentiation. Thus, any satisfactory explanation of the red tide must take into account their diverse physiological characteristics.

The conditions necessary for the growth of phytoplankton and for its maintenance include proper temperature, salinity, dissolved oxygen, illumination, hydrogen-ion concentration, the presence of mineral nutrient salts, and possibly of organic substances as well as other less known factors. In the ocean, under normal conditions, the quantity of nutrient salts, particularly the phosphate-phosphorus content, is believed to be the factor limiting the growth of phytoplankton, although the role of organic nutrients cannot be dismissed as unimportant.

The areas in which the outbreaks of red tide occur in the Gulf of Mexico are those where normally a low plankton content is coupled with o low phosphorus content (Smith 1949). In the red tide waters of 1946–47, Ketchum and Keen (1948) discovered that waters containing a dense *G. brevis* population have 2½ to 10 times the maximum total phosphorus concentration, both organic and inorganic, to be found normally in the Gulf (table 1). Dissolved oxygen, salinity, and other conditions deviated little from the average for the areas involved.

TABLE 1.—*Phosphate-phosphorus determinations (Smith 1949)*

Location	Date	μ gram-atoms/L
North side of Big Bird Key, Terra Ceia Bay, R. H. Williams.	June 3, 1946	4.80
Middle of Terra Ceia Bay, R. H. Williams	do	3.60
East side of Green Key, Hillsborough, R. H. Williams.	June 4, 1946	12.00
One mile west of Oreen Key, Hillsborough Bay, R. H. Williams.	do	8.40
Neighborhood of Sarasota, B. H. Ketchum	July 1947	4.5 to 7.4

The source of this increased phosphorus is the main problem faced by the red tide scientist. Smith (1949), Ketchum and Keen (1948) suspect that the presence of this element can be explained by a simple process of accumulation. If the initial absorption of phosphorus by *G. brevis* takes place over an entire water column (approximately 10 meters in depth), it is possible for the organism to concentrate this element by migrating to, and aggregating at, the surface. Unfortunately, chemical analyses of the water at different depths were not made, hence, no direct evidence is available to test this hypothesis. It appears that even with the removal of all the phosphorus from the water column, the phosphorus content was excessive. George L. Clarke of Harvard (personal communication) theorizes that vertical migration linked with a subsequent horizontal concentration due to convergences of water masses may be the complete solution.

Coincident with the large amount of total phosphorus the total nitrogen in red tide waters bears consideration. Sverdrup et al. (1942), indicate that the ratio of nitrogen to phosphorus in phytoplankton is about 15 atoms to 1. Although no analysis for this element was made, its presence or absence has a bearing on the problem. In order to provide for the large quantity of nitrogen that ordinarily accompanies the metabolic absorption of phosphorus, it is possible that red tide organisms might be able to utilize atmospheric nitrogen as some of the blue-green algae are capable of doing. On the other hand, if this is not so, the organism must be able to survive and develop under far lower nitrogen concentrations than ever before were recorded.

King (1950), while attempting to produce red tide in the laboratory, states that *Gymnodinium simplex*, a dinoflagellate closely related to *G. brevis*, was able to utilize dissolved organic nitrogenous matter. Though the concept of organic utilization by obligate phototrophs is not a new one to the field of protozoology (Lwoff 1947), it does suggest that in red tide dissolved organic material could be a source of nitrogen.

The concentration of nutrients may have been the result of the lateral or vertical migration of some organism or organisms other than *Gymnodinium*. Coincident blooming of other phytoplankton was pointed out by Gunter et al. (1948). These were primarily naviculoids and other diatoms. Utilization of phosphorus accumulated this way and later released could account for the bloom of the death-causing *Gymnodinium*.

The theory of accumulation as it stands does not explain the fact that swarming occurs at infrequent intervals as much as 30 years apart, nor does it explain any possible causative mechanism.

The upwelling of nutrient–rich water has been proposed but is not known to occur normally in the Gulf of Mexico. For red tide in other areas of the world, such as along the coast of Peru, this is an adequate explanation. However, the phosphorus present in the Gulf as reported by Ketchum and Keen was far in excess of that found normally in deep water. Nor are the deeper water layers of the Gulf rich enough in nutrient content to provide the amount found.

The presence of nutrient salts in bottom sediments is a likely source of nitrate and phosphate concentrations. Recently, Robert H. Stewart, a government geologist, in 1950 discovered phosphate deposits covering a 25-mile area off Tampa, Florida. Unfortunately, he has not supplied the authors with any further information. The coincidence of these deposits with the area in which red tide outbreaks have occurred suggests that this may be a partial explanation of phosphorus availability.

The problem presented is to account for periodic releases of nutrient salts from these bottom deposits. Possible explanations include shifts due to cataclysmic upsets in the ocean bottom or simple mechanical shifting of bottom muds due to strong bottom currents. These, of course, are still speculative.

River drainage as a source of mineral deposits in the Gulf has been suggested (Smith 1949). Since Florida is a major source of rock phosphates, this possible origin cannot be discarded. The remoteness of places like Key West and Cape

Sable from river drainage areas where rich phosphate deposits are known to exist renders this explanation doubtful. Ocean drifts seem to be northward in the region involved, though information on shore circulation and surface wind drifts is lacking.

The problem of the red tide as presented leaves a great deal of room for scientific investigation. The physiology, metabolism, and tactic responses of *Gymnodinium brevis* must be understood, and the source and mode of distribution of increased nutrients determined before it is possible to suggest a solution or remedy.

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SKETCH OF THE CHARACTER OF THE MARINE ALGAL VEGETATION OF THE SHORES OF THE GULF OF MEXICO

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GENERAL NATURE OF THE FLORA

The warm tropical current from Central America sweeps between Cuba and Yucatán to find its way into the Atlantic between Florida and Cuba or to swing into the Gulf of Mexico. With this as a striking feature of the environment, it is natural to expect, and to find confirmed in fact, that the marine algal flora is altogether tropical in character. Countercurrents alongshore do not carry northern plants southward. Where species known in the north are found here, they are ubiquitous types which range widely into the American tropics. Though much of the coast with which we are concerned is above the Tropic of Cancer—indeed all of the United States coast—where the land climate is no more than subtropical, this does not alter the character of the marine vegetation. The tropical currents from the southeast determine what species can migrate here, and the limited physical variety of much of the shore determines what species establish themselves. One may justly contrast the conditions at the Bermudas which, though in a much more northern latitude, are affected by the northward effluent stream through the Straits of Florida and have a highly varied shoreline and a similar, though much richer and more diverse, tropical marine vegetation.

Within our range one may generalize by saying that the most varied algal flora exists on the eastern shores, the Florida Keys certainly, and probably Cuba and Yucatán, and that as one progresses toward the north the flora becomes simpler and less spectacular. This is due, in part, to the physical nature of the shore, in part to the somewhat lower water temperatures and lower concentration of nutrient materials, and in part, at least locally, to the dilution of the sea water by the great rivers which empty into the Gulf in this sector.

MARINE BOTANICAL STUDIES OF THE GULF OF MEXICO

Studies of the algae of the shores of the Gulf have been so very few that, alone, they would hardly serve as a useful base of reference for the beginner. Nevertheless, they are adequate to show the main peculiarities of the flora, and by supplementing these lists with the more comprehensive literature of the West Indian islands one may approach the identification of Gulf algae with confidence.

Bounding our area on the east lies the Florida Peninsula and its appendage of keys. The eastern coast of this and the keys have been given quite a little attention. The first significant list of the algae of Florida is that of Bailey (1848) which was amplified and made much more useful a few years later by the illustrated volumes of Harvey (1852–58) and the more complete list of Farlow (1875). The bulk of the information to which this development was due came from the collection of Mrs. F. A. Curtiss (A. H. Curtiss, 1899) and Mrs. G. A. Hall who collected extensively and sent valuable series of plants to Harvey, Farlow, Collins, and experts abroad. Murray (1888–89), in bringing together all the lists of West Indian algae, included many references to those of Florida, and Collins et al., in their exsiccata (1895–1919) and his account of American Chlorophyceae (1909–18), greatly enhanced our knowledge of Florida algae.

However, it is obvious that these collections and records were of east-coast observations; though they include Key West, they give us practically no knowledge of the flora of the Gulf side of the peninsula. The writer (1928) was able from his study of the algae of the Dry Tortugas to greatly amplify the records from the Florida Keys in an area as much related to the Gulf as to the Straits of Florida, but only in a later (1936) paper did he specifically treat of a few west Florida records. Nielsen and Madsen (1949a, b) and Madsen and Nielsen (1950) have recently extended considerably the records of northwest Florida species.

Westward to Texas the coastal flora is essentially unknown. There are no lists of importance and only occasional mention of algae in botanical works (Cox 1901, Taylor 1936). The Texas

coast, fortunately, has received a little attention. A long-neglected set of specimens collected by A. C. V. Schott in 1853–65 came to the attention of the writer. It fell to him to publish on them (1941b), as he had previously studied recent collections by E. U. Clover, E. L. Cheatum, B. Smith, and C. T. Reed (Taylor 1941a).

Mexico entered the algal records early, with the Yucatán collection of Liebmann (Agardh 1847); numerous other specimens were in the Schott collection when it came to the attention of the writer (1941b); and he has studied Yucatán material collected by W. C. Steere (Taylor 1935). Other than in these three papers the algae of the Gulf coast of Mexico are unreported.

Finally, our information regarding the Cuban algal flora is slight. More than a century ago Ramon de la Sagra (Montagne 1842) listed 52 species, which was very creditable for the time. Farlow (1871), reporting on the collections of Wright, and Castellanos (1945) have dealt with the flora in general terms, while Howe (1918), writing on specimens of the *Tomas Barrera* Expedition, the writer (1941b), on the collections of Schott, and Sanchez Alfonso (1930) with material from the Havana area, have added numerous others. Curiously, the three detailed lists all deal with the flora of the Gulf sector of the coast.

Respecting work in progress from which future publications may result, it is known that collections have been made in Texas toward an amplification of the known flora of that State. We badly need information on the Mexican sector eastward, Dr. Francis Drouet and Dr. E. Y. Dawson have both collected substantially on the shores of the Gulf, and the latter from Cuba as well, and this material should add much to the exactitude of our knowledge. The Louisiana-northwest-Florida sector, while probably producing only a limited and specialized flora, still needs study. Extension of the Nielsen-Madsen reports would help with respect to northwest Florida. The richer west coast of peninsular Florida (like the northern east coast) needs active field work. Cuba is almost completely unknown and will prove rich in variety, though probably few novelties are to be expected. The writer has in manuscript an account of tropical flora, Gulf and Caribbean, for which many illustrations have been drawn, but early completion of this is not expected because of the hope of filling obvious gaps in our knowledge of the botany of the area. In short, the Gulf coast is the least known, as to marine plants, of the mainland coasts of Mexico and the United States.

COLLATERAL WORKS OF REFERENCE FOR THE GULF ALGAL FLORA

Recognizing the absence of any contemporary text to which we can turn for direct information on Gulf algae, we must consider the floras of neighboring areas that are most reliable and helpful in analyzing the flora of the Gulf itself. It is possible to set up a small working reference shelf, provided the books can be obtained. Therein lies the chief difficulty. Most of them are out of print and seldom appear in the catalogs of secondhand dealers.

One must distinguish between primary sources of the descriptions and figures of marine algae which have been found in the Gulf area and such floristic works as may be useful for the identification of specimens in general collections. For the former, we must refer to such works as those of J. G. Agardh (1872–90, 1892–99), of Harvey (1852–58), and the scattered notes of Howe (1905–09). Monographic works dealing with tropical genera will, in many cases, be needed, as those of Barton (1901) on *Halimeda* and the Gepps (1911) on other Codiaceae in the *Siboga* reports, and of A. Weber-van Bosse (1898) on *Caulerpa* from Buitenzorg. For early illustrations, not only these but the famous and regrettably rare *Tabulae Phycologicae* of Kützing (1845–71) will frequently be consulted. For the second purpose, we turn to local floras.

The most complete West Indian reference work is that of Børgesen (1913–20) on the former Danish West Indies. Its critical notes and numerous illustrations are very valuable, but keys and formal descriptions are not provided. Howe's algal flora of the Bahamas (1920) gives keys to some difficult genera, but generally not species descriptions or illustrations. Collins and Hervey (1917), in their Algae of Bermuda give, in addition, critical notes and much useful information on algal habitats, and Collins (1909–18) treats the Chlorophyceae adequately, with keys and brief descriptions. Hoyt (1920), writing of the Beaufort, N. C., algae, deals with some species also found in the Gulf and gives keys, descriptions, and illustrations. The present writer published, in

1928, an account of the algae of Florida, now urgently in need of revision but giving keys, descriptions, and many illustrations. Some of the needed changes were incorporated in his notes on Caribbean Marine Algae . . . (1942), where keys and additional illustrations are given. For Myxophyceae, Tilden's volume (1910) is still the only general American source, but this will need to be supplemented and corrected by that of Geitler (1932) and the current publications of Drouet. Outside of these few works, the investigator must rely on the great *Sylloge Algarum* of De Toni (1889–1924) and on a few score of brief papers scattered through botanical journals.

The chief reference collections containing algae of the species found in the Gulf are easily designated. Most generally available are those distributed in Collins, Holden, and Setchell's Phycotheca Boreali-Americana (1895–1919), of which numerous sets are held in institutions about the country, but in the use of these exsiccatae the usual attention must be given to corrections in nomenclature and identification. Many Florida algae appear in this series. The main Curtiss collection is in the U. S. National Herbarium. Because of his early dominance of phycological studies in America, Farlow accumulated valuable early reference materials at Harvard University. Howe did far more field work himself and acquired Collins' personal herbarium for the New York Botanical Garden so that the Gulf collections there are the most extensive in the country. The writer in his personal collections and the herbarium of the University of Michigan has a most valuable resource. While no other collections in this country contain many specimens from this area, one may list the very important herbaria at the University of California and the Chicago Natural History Museum, both of which have useful auxiliary collections.

CHIEF TYPES OF ALGAL VEGETATION

Since for great stretches of the Gulf coast no lists have been published, it is impossible to tabulate known floras. By describing here the more striking floristic elements of a few selected types of locality, it is hoped that future students may, through these characterizations, be guided in what to expect under similar conditions.

SHIFTING SANDY BEACHES AND ESTUARINE MUD FLATS

The great extent of the Gulf coast line which consists of unconsolidated sand and mud militates against the production of a complicated flora. Where every wave turns over the sand or stirs up a cloud of mud, algae do not colonize. Few microscopic forms are able to live mixed with the unstable sediments; few large species long survive adrift above them, and these accidental elements constitute no real flora. Such a region, regardless of the chemical nature of the sediments, is consistently an algal desert. The great areas of recently transported silt in estuarine regions and deltas are equally barren.

STABLE SAND AND MUD; POOLS, SMALL LAGOONS, AND COVES

When such sediments become stabilized, a different situation is presented. If the tidal rise and fall is considerable, broad zones of beach which were immersed at high water of spring tides are exposed at times of neap tide and such zones may show an algal flora. If they receive enough moisture from salt-marsh pools by percolation, or from rain or by other means, they may support a considerable and recognizable vegetation of such Myxophyceae as *Lyngbya aestuarii* and *Microcoleus chthonoplastes*, or on the surface mats of *Rhizoclonium riparium*. Such a vegetation may even be able to survive a little gentle wave action undisturbed. Where silt transported by stream movement in flood is left stable by recession, it, likewise, may develop similar colonies in brackish estuaries.

When waves throw up barrier beaches of calcareous sand and coral rubble, pools, or lagoons are cut off in which surf action is absent and tidal action greatly reduced or eliminated. Rains serve to dilute the water, especially at the surface. On sunny days, the temperature rises greatly. Under such circumstances, few algae except Myxophyceae can survive, but at times these form a heavy sludge over the bottom, where *Chroococcus turgidus*, *Gomphosphaeria aponina*, Oscillatorias, and Lyngbyas dominate. If there is a direct communication with the sea and some circulation, if the area is relatively large, and especially if there is a moderate depth of 3 to 12

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dm. of water at low tide, then colonization by marine vascular plants, such as *Ruppia maritima* L., *Halodule wrightii* Asch., or perhaps *Zannichellia palustris* L., may occur, and the flora resembles that of the next section. With or without this colonization, the growing conditions are so greatly improved that many larger algae grow in abundance. The Myxophyceae form larger masses of such coarser species as *L. majuscula*, and on the vascular plants occur epiphytic growths of other species, Myxophycean, diatomaceous, or of larger types, inconspicuous in form and color but very general.

PROTECTED COVES AND POOLS WITH A MARINE CHANNEL

The numerous deeper pools near the edges of salt marshes partake of the character of these ponds barricaded from the sea, though they may show a distinctive growth of algae including *Bostrychia rivularis*. Others receive too much fresh water to have a well-developed marine flora, while on the contrary yet others are more like protected coves.

The floras of these smaller coves vary greatly one from another, but no one in itself shows much range. One will have the bottom studded with *Penicillus capitatus* (fig. 48–d), another will be dominated by *Thalassia testudinum* K. & S., or *Halodule*, bearing epiphytes, another by *Amphiroa fragilissima*, by *Spyridia filamentosa*, or by *Gracilaria confervoides* (fig. 50–e). This last is sometimes exceedingly abundant and is harvested commercially for its gel content. It is about the only economically important alga recognized in the area. Others have advantageous features of their own, however, and await the discovery of harvestable quantities.

PROTECTED BAYS AND LAGOONS

The transition from these small coves to large ones, to protected bays and lagoons, is easy and is accompanied by an increase in the variety of the marine flora. In shallow water the same species are found and many others in addition. Characteristic is the excellence of vegetative development of all the plants whenever there is a good circulation of sea water. On the other hand, even if the lagoon is large, a muddy bottom and a reduced communication with the sea generally will be reflected in a poor flora of Myxophyceae and a few Chlorophyceae. Under good conditions, *Sargassum* is tall and freely branched, *Ectocarpus* and *Padina vickersiae* flourish, as do *Acetabularia crenulata* (fig. 48–a), *Batophora oerstedi*, *Cymopolia barbata*, *Codium decorticatum*, *Udotea flabellum* (fig. 49–e), and many other Codiaceae and Caulerpas, especially *C. racemosa* (fig. 49–c) and *C. sertularioides*, which form magnificent colonies. A great many of the species common on the more open rocky coasts and reefs may appear here, more luxuriant and loosely branched than elsewhere. The list is too long to give here, but it points sharply to a greater variety in the Florida Keys sector and a poorer one on the northern shores of the Gulf.

The larger area of these bodies of water involves the occurrence of natural or artificial rock or concrete walls, jetties, piers, or other solid structures which afford a new type of habitat, and here an intertidal zoned band will often be recognized in which *Enteromorpha*, *Caloglossa*, *Catenella*, and especially *Bostrychia tenella* will generally be conspicuous features.

MANGROVE THICKETS

These lagoons, inlets, and coastal islands may, in some localities, especially in southern Florida, be bordered or even nearly filled by mangroves, primarily *Rhizophora mangle*, with *Avicennia nitida* higher along the shore. The prop roots of *Rhizophora* and the pneumatophores of *Avicennia* offer excellent support for algae, and a strongly developed belt of *Bostrychia tenella*, or even more conspicuously *B. montagnei* (fig. 50–c) may encircle each root, with *Polysiphonia macrocarpa* a little lower down, while on emerging ground which receives a little sunlight between the mangroves there may be a green mat of *Vaucheria* or a mossy growth of brighter *Cladophoropsis membranacea*. Around the border of such a thicket where light is ample, a few species of other larger algae may grow luxuriantly attached to the submerged parts of the roots, as *Padina vickersiae*, but the flora of mangrove thickets is not marked by great variety.

TIDAL STREAMS

Tidal streams commonly discharge through these protected coves and thickets. Their flora is largely determined by the light received and the admixture of fresh water. Near the mouth, marine Myxophyceae, *Vaucheria*, *Enteromorpha*,

FIGURE 48.—*a*, *Acetabularia crenulata*, several plants, × 0.4; *b*, *Cladophora fascicularis*, a small portion of a branch, × 0.8; *c*, *Enteromorpha flexuosa*, several plants, × 0.7; *d*, *Penicillus capitatus*, a young and a mature plant, × 0.4; *e*, *Codium dichotomum*, a small portion of a clump, × 0.2; *f*, *Ulva lactuca* var. *rigida*, a single plant, × 0.4. Drawings by C. V. Cangemi.

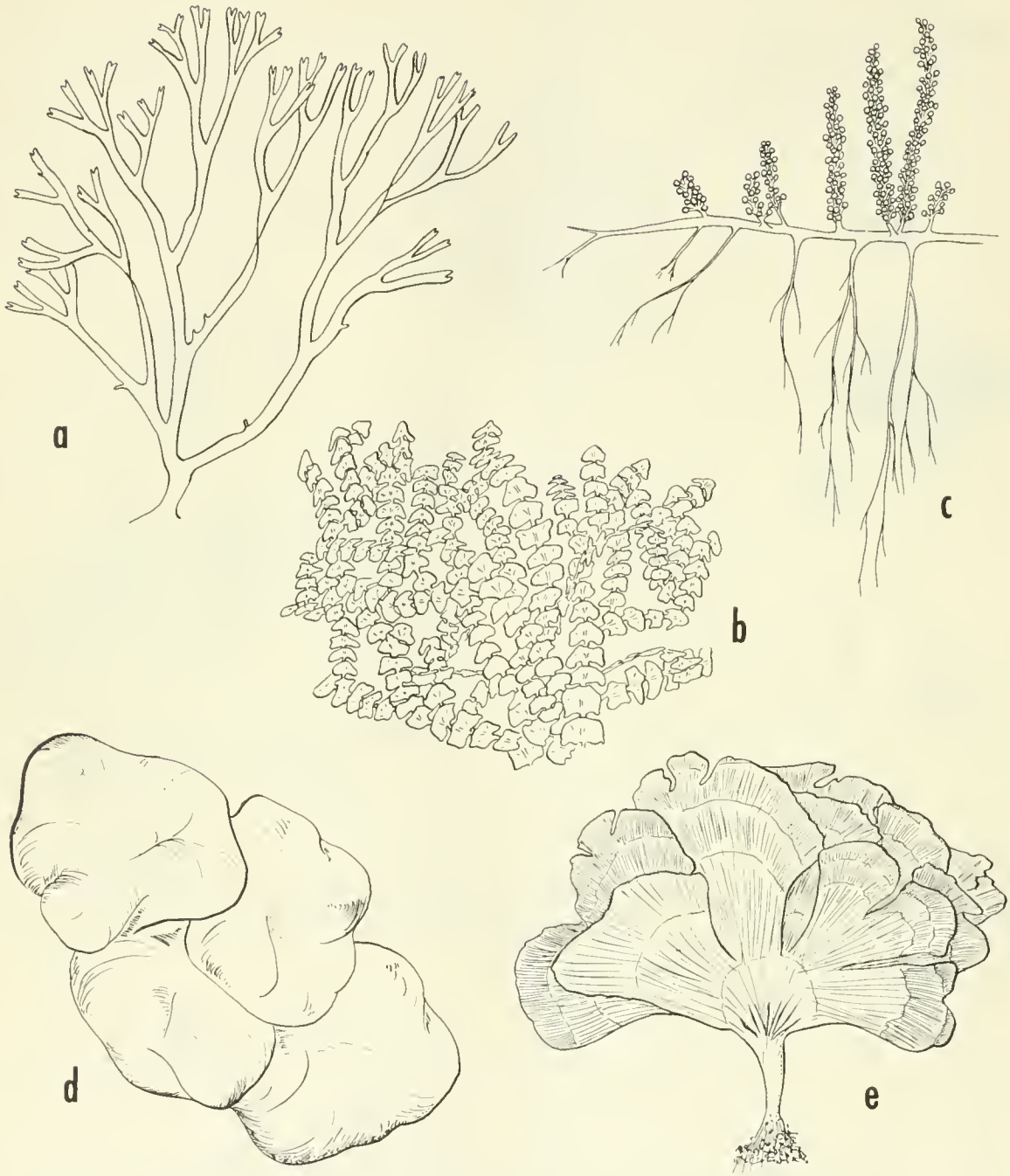

FIGURE 49.—*a*, *Dictyota cervicornis*, a small portion of a plant, × 0.7; *b*, *Halimeda opuntia*, a small portion of a clump, × 0.4; *c*, *Caulerpa racemosa*, portion of a stolon with erect green branches, × 1.3; *d*, *Colpomenia sinuosa*, a single plant, × 0.4; *e*, *Udotea flabellum*, a single plant, × 0.7. Drawings by C. V. Cangemi.

Caloglossa, and *Bostrychia* will generally be important, while much farther up, fresh-water genera including, particularly, the peculiar *Compsopogon*, will dominate. It is notable, however, how far upstream the adaptable genera mentioned may, in the absence of pollution, be found.

SANDY SHALLOWS AND "REEFS" OF SHELL AND CORAL RUBBLE

Shallow water among the keys combines the advantages of shelter from storms with ample water circulation, sunshine, and freedom from fresh water and mud. Sometimes similar sandy flats extend out far from the shore but are less protected toward the sea than those among the keys. Often the white coral sand is directly exposed and is only partly covered by the vegetation which is chiefly limited by the number of suitable objects on which algae may attach. Over the soft sand bottom the marine vascular plants may form vast "sea grass" meadows with *Halodule wrightii*, *Cymodocea manatorum* Asch. (manatee grass), and especially *Thalassia testudinum* (turtle grass) in shallow water, and with *Halophila baillonis* Asch., at a depth of several meters, generally 5 or more, exceeded by *H. engelmanni* Asch., which may go as deep as 75 meters, probably much more. While little grows on the *Halophila*, there may be a great variety of epiphytes on the *Thalassia* and other shoal-water types. Most ubiquitous of these are the thin encrusting species of *Fosliella*. Also common are species of *Spyridia*, *Hypnea*, small Laurencias and Chondrias, slippery brown *Aegira* and *Ectocarpus*, and many others. Nowhere is one feature of the subtropical and tropical marine flora, the extreme etiolation of the Rhodophyceae, more evident than on these sandy shoals. The Chlorophyceae are just as green here as elsewhere, the Phaeophyceae as brown, but the Rhodophyceae do not have much need for and so do not develop their phycoerythrin pigment, and their small proportion of green chlorophyll is not conspicuous, so their aspect is light and dull purplish to straw-colored.

Apart from epiphytes, many other algae grow in these "grass" beds. Mats of *Amphiroa fragilissima* are common as are scattered plants of *Penicillus capitatus*, *P. pyriformis* and *P. dumetosus*, *Avrainvillea nigricans*, *Udotea flabellum*, *Halimeda tridens*, and *H. monile*. Others, like the Caulerpas, rather tend to replace the "grass" beds as they have similar spreading rhizomes. While *C. sertularioides* and *C. cupressoides* may be commonest, other species also occur, such as *C. paspaloides* and particularly *C. prolifera*.

In more open water where "grass" beds are lacking, great beds of *Halimeda opuntia* (fig. 49–b) occur, a plant of different habit from its congeners, and, if large shells and coral fragments abound, many species typical of coralline reefs also find footing, particularly *Laurencia obtusa* (fig. 50–b), *Padina sanctae-crucis*, *Dictyota divaricata*, *Caulerpa racemosa*, *Batophora oerstedi*, and *Acetabularia crenulata*. The presence of a slight ridge or "reef" of shell fragments may, for instance, determine the presence of a striking local colony of *Acetabularia* or of its relative, *Neomeris annulata*.

ROCKY SHORES AND INSHORE REEFS

The area under consideration is exceptionally poor in tracts of rocky shoreline. The only portion of shoreline with such a substratum of whose algae we have any detailed account is that of south Florida, particularly the Florida Keys, where a certain amount of calcareous rock may lie at the waters' edge, and where old coral formations in shallow water afford even better attachments for algae. Equally promising stretches of shoreline occur in Cuba and Mexico, but of their productivity we have no detailed account. Marine algae do not flourish in tracts preempted by vigorous, actively growing corals and gorgonians. It is on these older reefs, on submerged structures built of stone, and in lesser degree on concrete, wood, and iron structures, that the vegetation gives us our chief view of algae suited to these stable anchorages. Through much of Florida and all the north and northwestern sectors only these artificial structures support what in a completely natural state would only occur as lithophilic colonies, and being relatively recent, small, and scattered, the variety of plants they support is far less than one would expect on the rocky shores of West Indian islands.

In dealing with so great a coastline, much quite unknown as to vegetation, and considering all seasons of the year, it is impossible to be specific as to algal communities, though some suggestions can be made. If circumstances permit, the upper zone of algal growth will be one of marine Myxophyceae in a black or olive crust, with below it very usually a clear zone of *Bostrychia tenella* or

FIGURE 50.—*a, Sargassum natans*, a small portion of a plant, × 0.4; *b, Laurencia obtusa*, a small portion of a plant, × 1.0; *c, Bostrychia montagnei*, a small portion of a plant, × 1.0; *d, Digenia simplex*, a portion of a large plant, × 0.8; *e, Gracilaria confervoides*, a small portion of a plant, × 0.7. Drawings by C. V. Cangemi.

B. binderi, more or less intermixed with *Enteromorpha* (fig. 48–c) and *Rhizoclonium*. Green turfs of *Cladophoropsis membranacea* and darker ones of *Cladophora fuliginosa* may be close by, with mats of *Wurdemannia miniata* and closer-attached *Gelidium pusillum*, but *Catenella* and *Caloglossa* are less important than in localities discussed earlier. Seasonal growths of *Colpomenia sinuosa* (fig. 49–d), *Hydroclathrus clathratus* and perhaps *Codium intertextum* are to be expected near the low-tide line, with *Laurencia papillosa* and *Sphacelaria*, stunted *Sargassum*, *Amphiroa*, and *Centroceras*.

At levels primarily submerged or laid bare only by the backwash of the waves, we have a richer and sometimes spectacular vegetation. Near the surface a new group of Chlorophyceae appear: *Caulerpa racemosa* and *C. verticillata*, *C. sertularioides*, *C. cupressoides*, *Dictyosphaeria cavernosa*, and *Dasycladus vermicularis* on the rock faces, *Anadyomene stellata* and *Valonia macrophysa* more in crevices or other protected spots. We also have such Phaeophyceae as *Ectocarpus duchassaignianus*, *Pocockiella variegata*, and Dictyotas. Somewhat deeper, we may have the brilliant peacock colors of great masses of *Zonaria zonalis*, and at this level, abundant Padinas, Sargassums, *Cladophora fascicularis* (fig. 48–b), and more Dictyotas, among which *D. cervicornis* (fig. 49–a), may be the most common, but *D. ciliolata* and *D. dentata* will reach the greatest size and are often irridescent. Here, also, come a few species of conspicuous Rhodophyceae, Galaxauras, and Liagoras, with lower down *Heterosiphonia wurdemanni*, *Centroceras*, and *Spyridia* in masses, and some showy Halymenias. The number of other kinds at this and nearby levels makes continued detailed listing unprofitable.

PELAGIC SEAWEEDS

The fact that the term "gulfweed" for our drifting algae has arisen at all is suggestive of the conspicuousness of these plants in our area. Although the term has long been known, one has come to think of these plants more in relation to an ill-defined "Sargasso-Sea" in the North Atlantic. However, while the abundance of the "weed" in the Sargasso Sea is perhaps greater than in the Gulf of Mexico, the amount is nevertheless considerable in the northwestern parts even if less conspicuous in the literature. The best general account of the distribution and ecology of the gulfweeds is that of Parr (1939), and it particularly deals with *Sargassum* as found in the Gulf. The taxonomic segregation of the Gulf and the Caribbean benthonic and pelagic species is far less difficult than that of the Pacific species but still is exceedingly confusing to an inexperienced student of them. The books mentioned for the general flora will clear up most points; the summaries of information regarding the species of the world in DeToni (1895) and Grunow (1915–16) will be necessary to the advanced student.

First of all, it is to be recognized that the benthonic sargassums are particularly suited to transport by currents once they come adrift, and any such species may travel among the driftweeds for a long distance from their origin. Thus, *Sargassum hystrix* v. *buxifolium* has been collected on the coast of Nantucket among gulfweeds as a very exceptional occurrence (1938, for example). However, the new growth on these plants is not so altered from the parts developed during the attached growth period as to resemble the pelagic species. Of these, there are two: The classic *Sargassum natans* (L.) J. Meyen (fig. 50–a) and *S. fluitans* Børg., each somewhat variable. However, the former has much narrower leaves with more terete teeth than the latter, and the vesicles are characteristically long-apiculate. While the leaves of *S. natans* never have cryptostomata, rudiments of them may occasionally be seen in the latter species. Neither has been convincingly reported in fruit, contrary to the common state of mature benthonic plants. Parr (1939) reports that significant amounts of drifting gulfweed are not found south of a line extending from approximately the latitude of 16°–17° near the Lesser Antilles to 14° near the Central American coast. We may accept it that there is very rapid growth and fragmentation of the floating plants north of this line, and there is no evidence that the pelagic flora needs to be initiated by a constantly replenished nucleus of benthonic origin. Both species of gulfweed, passing out through the Straits of Florida, continue in excellent health into the drift area called the "Sargasso Sea" and multiply vegetatively there. The wind and the water currents also bring the sargassums into the Gulf of Mexico. While there seems to be some growth of the plants within the Gulf, especially during the summer, it is clear that it is not very considerable, and the flora comes to consist of

more than 90 percent *S. natans* which gradually passes into an unhealthy state, particularly in the latter part of the year and in the more northwesterly area.

LOCAL FEATURES OF THE GULF COAST MARINE ALGAL FLORA[1]

Since the algal vegetation of most of the shoreline of the Gulf of Mexico has not been studied, a review of what has been done is in order and an application of the information derived from this to the rest of the coast. Such an analysis will show what work needs to be done and what areas may be expected to yield the greatest rewards.

The Florida Keys, as far as we yet know, support much the richest algal flora in our area. About 400 species of marine algae are known from the State, and most of them have been found among the Keys. The fact that intensive study has been limited to the Dry Tortugas was a matter of chance; probably the other more exposed Keys are equally rich. Fortunately, a very helpful study of the littoral ecology of these islands has recently been presented by the Stephensons (1950) which relates the plant and animal components. The presence of offshore corals, in itself, is of no present advantage because algae do not grow to any extent on living corals, but the older portions of reefs, dead masses of coral rock and debris form an excellent foundation for algal colonies. Many spectacular ones appear: great beds of *Halimeda opuntia* and Caulerpas in shallow water, of living brown and white *Padina* fans, golden clumps of Dictyotas and iridescent *Zonaria zonalis* a little deeper. In the next lower depths and in shaded areas, a great variety of "red" algae appear. Beach rock outcrops, the foundation and moat of Fort Jefferson, wide stretches of soft muddy sand, ridges of shell and small coral fragments, all have special advantages and are favored by particular species, as discussed elsewhere. The proximity of the Gulf Stream to the east gives good circulation of the water, and at times an abundance of the species of pelagic sargassums is evident.

When one crosses Florida Bay to Cape Sable one leaves behind the area of most favorable growth conditions, and the floras around the Gulf are thenceforth restricted ones. The west coast of Florida, without the advantage of a strong offshore current and considerably encroached upon by the red mangrove, *Rhizophora mangle*, offers a less favorable habitat which continues unimproved for many miles to the north since only at isolated spots such as Cape Sable, Pavilion Key, and Marco are large sandy beaches reported and no extensive suitable rocky shore. In the Florida Bay area Davis (1940) reports turtle grass with *Acetabularia*, *Caulerpa*, and *Gracilaria* growing among the pioneer *Rhizophora* colonies. The mangrove roots may well support the typical *Bostrychia* vegetation, some suitable mud-favoring species like *Penicillus* may occur in the shallow open areas, but the vegetation is not likely to be a rich or varied one for neither these inshore features nor the sand of the offshore islands favor any variety of algae. The Ten Thousand Islands area is especially characterized by the great development of red mangroves over much shell and marl beneath with beaches showing on the largest islands (Davis 1940). A collection made at Naples shows a poor flora of *Enteromorpha*, *Ectocarpus*, *Spyridia*, and the like. The configuration outside Fort Myers and Punta Gorda promises better conditions, but we have no reports, and the amount of fresh water discharged may restrict the flora. The Tampa Bay area is certainly different, for rock outcrops, as on Hillsboro Bay, locally offer a good substratum for algal growth. Limited though the collections we have seen have been, they certainly indicate that there is a good, though not very complex, shallow-water flora of well-developed specimens. However, a good deal of the shoreline is sandy or of shell reefs, with considerable mangrove thickets, and proceeding northward we again come upon an inhospitable, swampy coast. From Cedar Key, we have received collections indicating a rather limited flora but by no means an extremely reduced one including several typical tropical genera like *Codium*, *Caulerpa*, *Padina*, *Laurencia*,

[1] Owing to lack of personal familiarity with most of the Gulf coastline and the fact that published marine botanical studies are generally lacking or poorly documented, the writer has appealed for help and information to several persons, many of whom are not botanists, but each is well informed regarding some part of the coast. Among these may be mentioned with especial gratitude: Professor Clair A. Brown, University of Louisiana, Baton Rouge, Dr. P. A. Butler, Fish and Wildlife Service, Pensacola, Fla., Professor John H. Davis, University of Florida, Gainesville, Dr. Francis Drouet, Chicago Natural History Museum, for the northern shores of the Gulf, Dr. Joel W. Hedgpeth, University of Texas Marine Station, Port Aransas, Roy N. Jervis, University of Michigan, for the Cuban coast, Director of the Herbarium, Hno. León, Colegio de la Salle, Habana, Cuba, Professor W. Armstrong Price, Agricultural and Mechanical College of Texas, College Station, Dr. Paul Weaver, Houston, Texas, for the Mexican coast, and Professor R. H. Williams, University of Miami, Coral Gables, Fla.

and *Digenia*, with genera which, like *Hypnea* and *Gracilaria*, are suited to and widespread in warm, quiet water. On a nearby rocky causeway appear *Ectocarpus*, *Caloglossa*, and other Rhodophyceae and marine Myxophyceae, but apparently Dasycladaceae are already few and do not go much farther.

From this point the red mangrove ceases to play a significant part in the shore vegetation, and the black or *Avicennia* mangrove which is present but not exclusive to the South takes over and continues, somewhat reduced in stature, around the coast. The pneumatophores of *Avicennia*, like the prop-roots of *Rhizophora*, can support a *Bostrychia-Caloglossa-Catenella* algal association but arise from the tidally immersed mud for only a few inches and do not extend out into water of more than a very slight depth. While the flora here includes an abundance of *Gracilaria* and other mud-favoring, widespread types, there are still many characteristically tropical species.

North and west of Cedar Keys the algal flora changes much for the worse owing to the unfavorable factors suggested earlier. Although *Batophora* has been reported from Adams Beach and *Acetabularia* from near Panama City, the family Dasycladaceae is now unimportant. The last records of Caulerpas and Codiaceae are from about Apalachee Bay. Unfortunately, the data for Phaeophyceae and Rhodophyceae are not so sharp, for the more distinctive, less cosmopolitan types disappear early as we go up the coast. The remaining flora of *Gracilaria* and *Hypnea* in protected bays, of *Bostrychia* and its associates on the mangrove roots, with Ulva (fig. 48–f), Enteromorpha (fig. 48–e), and Myxophyceae, dominates the vegetation throughout the northern arc, so far as it is known. As studies progress with the establishment of marine laboratories, doubtless numerous other species will be recorded, and more exact details will become available, but the general pattern probably will not change, i. e., nowhere will a diversified flora of conspicuous species appear. Near Carrabelle there is some *Thalassia*, and some associated small forms like *Fosliella* may be expected. Near and a little west of Pensacola considerable growths of attached *Sargassum* are reported. However, this district represents the outpost of numerous things, for on causeway rocks east of here *Bryothamnion*, *Laurencia*, and other tropical Rhodophyceae appear. This is our last reported outpost of *Catenella* of the mangrove association. Still, the most characteristic red algal flora is that of the bays and swamp mangroves associated with Ulvaceae and blue-green algae.

Alabama's short coastline is phycologically little known. There seems to be some growth of *Polysiphonia* where it can become attached. *Sargassum*, apparently the pelagic gulfweed, is washed ashore in the Mobile area. More conspicuous on docks, walls, and such constructions are growths of *Enteromorpha*, *Rhizoclonium*, and blue-green algae, but there is very little natural opportunity for coarser algae, and these forms adapted to mud are the most widespread.

Mississippi is in the same unreported condition. There is much shoal water off shore. The coast is guarded by a line of sandy islands, and itself is of sand and mud with some swamp areas approaching the shoreline to the west. The flora reported is limited to observations about Biloxi, Ocean Springs, and Bay St. Louis. The flora is much the same as in Alabama and restricted by the same factors except that we have no reports of *Sargassum*, though doubtless gales can throw gulfweed ashore upon the outer islands.

In fact, the general limitation of the algal vegetation of the north and northwest sector has now been completed. The prevalence of muddy shores will explain the dominance of a flora composed of *Rhizoclonium*, *Vaucheria*, and numerous Myxophyceae. For a long distance to the west this is seldom relieved by sandy beaches. Occasional accumulations of shells permit the appearance of *Enteromorpha* and *Ulva* which can also grow on exposed roots and tree balks projecting from the mud. The exposed black mangrove roots permit the *Bostrychia-Caloglossa* vegetation to appear, often with elements from the last-named mud and shell flora. All these also appear on wharves and stone jetties but with almost none of the larger types added that flourish in like situations to the east.

Louisiana has a highly dissected coastline with swampy land almost everywhere descending to the sea. Off the coast between the Sabine and Atchafalaya Rivers just inside the 183-meter line, Trask, Phleger, and Stetson (1947) report flat-topped hills which rise to within 18 meters of the surface, and which in 18 to 36 meters of water support a dominating flora of *Lithothamnion* balls

associated locally with corals, a very remarkable flora to be discovered in this area. Offshore on the east the sandy Chandeleur Islands with shell ridges shield a shallow, sandy sound. Even marshy islands like Isle au Pitre to the northeast of the delta may be margined by beaches of shells. In the outer delta region at Grand Isle and near the western side of the State south of Lake Calcasieu we again have a sandy shore. Unstable sand subject to wave action is not favorable to growth of algae, and only the more sheltered muddy shores can maintain the flora outlined in the paragraph above. A particular feature of the tidal marsh streams emptying into the northern part of the Gulf may be introduced here. These are reported to support a flora similar to the above near the sea but with the very curious *Compsopogon* in fresher water. There is no reported work dealing with Louisiana marine algae, but considerable collections from the north Gulf coast are now being studied and will add to the details of this account. In salt marshes and tidal lakes on the Calcasieu River the usual limited flora prevails. Weeks Bay and the Canal are similarly but sparsely populated. Lake Pontchartrain on its southeast side is again similar but with more evidence of *Cladophora*, *Ectocarpus*, *Polysiphonia*, and *Bostrychia* where these are favored by rocks and wharf piles. On the north shore and at the east end, only *Rhizoclonium* and blue-green algae appear. The tidal marshes at the south delta extension of Chenier Caminada and Grand Isle show the usual flora including *Compsopogon*; on the outer beaches much *Sargassum* is washed ashore by storms. In the bay to the west the same flora occurs again, but by virtue of pilings and other firm attachments we have there the *Bostrychia* flora. In general, because the shores of most of the state are marshy, the opportunities for algal colonization are restricted.

A great change appears as one crosses the State line into Texas. Only a very short coastal section below Port Arthur is marshy; thenceforth sandy shores face the sea nearly everywhere. Immensely long and narrow peninsulas and islands line the coast with relatively shallow bays behind them. These unstable, sandy, outer shores discourage algae effectively, but in the bays behind and on the rocks of the jetties and other harbor structures a much enhanced (though still not a rich) flora appears, of 60 or more macroscopic species. The neighborhood of Galveston and Texas City yield few of these: *Ulva lactuca* (fig. 48–f), *Gelidium crinale* var. *platycladum*, *Agardhiella tenera*, and *Gracilaria confervoides* (fig. 50–e) slightly enrich the sparseness of the continued Louisiana type of marsh flora, and of these only the *Gelidium* really is additional to the Gulf north shore flora and only in its variety among the four seems at all tropical.

The next group of reported stations centers about Matagorda Bay and its offshoots; Schott, nearly a century ago (Taylor 1941a, 1941b), found it a profitable collecting ground. Here the flora again includes *Centroceras*, *Digenia simplex* (fig. 50–d), and less distinctive tropical additions. However, the flora between Copano Bay and Corpus Christi Bay is much richer. *Ulva fasciata*, *Cladophora fascicularis* (fig. 48–b), *Acetabularia* (fig. 48–a), *Batophora*, *Padina*, *Corallina cubensis*, *Ceramium subtile*, and Laurencias greatly accentuate the tropical character of the flora despite limited suitable substrata. It is not solely this feature which restricts the flora, of course, for the sandy to muddy inner bays might be suitable for Caulerpaceae and Codiaceae, not yet reported from the State, were it not for unrecognized limiting factors. Where muddy, the great shallows behind Padre Island may show an enormous development of an almost leathery blue-green algal flora. On the outer islands *Sargassum* is washed ashore in conspicuous amounts. This is partly, but not solely, of the pelagic species, for *S. filipendula* and *S. pteropleuron* are also reported. Otherwise, nothing distinguishes the flora hence to the Mexican boundary.

The marine flora of the east coast of Mexico is far less known than that of the west coast and both shores much less than the land flora of the central parts of the country. For the east coast this is not hard to understand. South from the Rio Grande extend sandy barrier islands which promise little of botanical interest. With the approach to the shore of hills containing calcareous rock the lime content of the sands increases progressively to Tampico. A little to the north at Punta Jerez limestone rocks outcrop in about 18 meters of water and corals occur, so algae may be expected. The calcareous content of the sands, in general, decreases again south of Tampico, but limestone is expected at Lobos Island and other reefs south of Cape Rojo. Lava materials rather

replace other elements near Punta Delgada, but as one approaches Veracruz sandy beaches appear, with numerous rocky shoals and reefs where Heilprin (1890) long ago confirmed the presence of actively growing corals and coral reefs (as at Gallega and Anegada de Adentro Reefs), as well as serpulid reefs (Punta Gorda and in part Hornos Reef), the presence of both of which suggests good conditions for algal growth. This had long before been recognized by Liebmann who collected here, from among whose algae Agardh (1847) described five striking species as new. Farther to the east at about longitude 95° W., lava flows account for a rocky coast with cliffs, but the sandy beaches begin again at Punta San Juan and extend until, at the Rio Tonala, mangroves take over and dominate the swampy, rather muddy coast to the Laguna de Terminos, a large body of water with several streams emptying into it and two major passes communicating with the sea. This should support an appropriate algal flora. Hence out the west coast of Yucatán, the presence of underlying limestone rock and the absence of streams substitute an irregular coast with much calcareous sand and mud derived from this rock. It is, curiously, from this unpropitious area that we get most of our few records of Mexican east coast marine algae. Several specimens were collected by Steere in 1932 at Progreso and reported by the writer (1935) together with odd specimens from other sources, especially some collected by A. C. V. Schott who visited Progreso, Sisal, and Celestum in 1865 and made very important collections, indicating that there was here a substantial vegetation characteristic of the Caribbean flora and of a rocky shore. Liebmann (Agardh 1847) had obtained a new *Sargassum* from the Campeche reefs only a little earlier. The Schott algal collections, of some 40 species, in general remained unknown until the present writer reported on them (1941b). Shoal water extends far off shore all along the north and west of the peninsula, and 45 miles off Celestum and Sisal in about 32 meters of water *Sargassum* is sufficiently abundant to appear on the naval charts as a distinctive feature occurring on a coral bottom.

Of Cuban algae, we know even less than we do about those of Mexico. Most of the island has never been surveyed for these plants. Small collections have been made from the Guantanamo area but not reported upon. Fortunately, three considerable lists (Montagne 1842, Howe 1918, Sanchez Alfonso 1930) do apply to the Gulf coast from Habana eastward to Cabo San Antonio. While doubtless only a portion of the flora is represented, it is clear that we have a typical Caribbean tropical assortment in accord with the varied coastline. For example, Mariel, west of Habana, shows a rocky limestone coastline beyond which sandy beaches alternate with rocky shores along the coast. Serpentine rocks are reported to reach the shore in some places. In many areas broad stretches of shallow water extend far out from the shore, and in such shallows near Habana *Thalassia* grows over the sandy bottom, doubtless with its attendant algae, and doubtless occurring also elsewhere along the northwest coast. Many parts of the shore are marked on charts as being mangrove-bordered, so the algae commonly associated with *Rhizophora* are to be expected. The western peninsula of Guanahacabibes is generally low on the north shore and mangrove fringed. A few miles off much of the northwest coast lie the Colorado Reefs, commonly at a depth of 2 to 5 meters, which presumably bear the rich tropical reef flora. Of the shores which face the Gulf of Mexico, Cuba has in its relatively small extent the most promising coast line and should rival Florida in the richness of its algal flora when fully explored.

CITED LITERATURE OF GULF OF MEXICO MARINE ALGAE AND BIBLIOGRAPHY OF PRINCIPAL WORKS ON COMPARABLE WEST INDIAN MARINE ALGAE

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FLOWERING PLANTS OF THE WATERS AND SHORES OF THE GULF OF MEXICO

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The maritime flowering plants of the Gulf of Mexico, because of their dependence on light to carry on photosynthesis and on the substrate to furnish a place of attachment for their roots or underground stems, are confined to shores and shallow coastal waters. No flowering plant has been reported from Gulf waters at depths greater than 100 meters. Taylor (1928) reports that *Halophila engelmannii* Aschers., a sea-grass, was dredged in the transparent waters of the Dry Tortugas area from measured depths up to 73.2 meters and one estimated depth of 91 meters. Thus only the margins of the Gulf of Mexico are of concern to one interested in vascular plants.

Knowledge of the flora and vegetation of the Gulf perimeter is mostly inadequate. Only in very limited areas such as the Florida Keys is information about the plant life extensive. Data on the Gulf maritime flora must be sought in many publications treating limited land areas fringing the Gulf. The appended bibliography attempts to bring together the more important and recent of these references.

Floristic works of the greatest usefulness in the Gulf region because of their wide scope and relatively recent publication are: Small's Flora of the Southeastern United States, 1913, and Manual of the Southeastern Flora, 1933, Leon and Alain's Flora de Cuba, 1947–51, and Standley's Trees and Shrubs of Mexico, 1920–26, and Flora of Yucatán, 1930. Pertaining to smaller areas but often containing much valuable information on the distribution of maritime plants are: Small's Flora of the Florida Keys, 1913, Mohr's Plant Life of Alabama, 1901, Lowe's Plants of Mississippi, 1921, Lloyd and Tracy's The Insular Flora of Mississippi and Louisiana, 1901, and Cory and Parks' Catalogue of the Flora of the State of Texas, 1938. Floristic and ecological treatments of still more limited areas are referred to under the several plant communities.

The marine and strand flowering plants of the Gulf are best considered in the natural groupings in which they usually grow. There are four such major plant communities: submarine meadow, mangrove swamp, salt marsh, and sand-strand vegetation.

SUBMARINE MEADOW

Least collected and studied of all the Gulf plants are the marine spermatophytes or sea-grasses. These aquatic flowering plants, members of the Hydrocharitaceae and Zannichelliaceae rather than true grasses, have received some attention in the waters around the Dry Tortugas. Bowman (1916, 1918) and Taylor (1925, 1928) have contributed original observations on the ecology and morphology of species in that area. For other parts of the Gulf information about them is scanty (Howe 1918; Davis 1940; Hotchkiss 1940; Stephenson and Stephenson 1950). Several authors (Ascherson 1906; Ostenfeld 1914, 1926–27; Setchell 1920, 1934a) have discussed their world distribution, and Balfour (1878), Rydberg (1909), and Bowman (1916) have contributed papers on their morphology. The most thorough taxonomic treatments of the marine spermatophytes are included in Ascherson and Graebner's (1907) monograph of the Potamogetonaceae in Das Pflanzenreich and Ascherson and Gürke's (1889) study of the Hydrocharitaceae in Die Naturalichen Pflanzenfamilien. Descriptions and keys for the identification of Gulf species are available in Small (1933) and Muenscher (1944).

More species of marine flowering plants are found in the Gulf of Mexico and Caribbean Sea than anywhere else in the Western Hemisphere. In the waters around the Florida Keys grow five species belonging to two families: *Diplanthera wrightii* (Aschers.) Aschers. and *Syringodium filiforme* Kutz., manatee-grass, of the Zosteraceae, *Thalassia testudinum* König, turtlegrass,

Halophila baillonis Aschers. and *H. engelmannii* Aschers. of the Hydrocharitaceae. *Halophila aschersonii* Ostenf., as well as the above, is found in the Caribbean and is reported as far south as Recife, Brazil. The widespread *Ruppia maritima* L., widgeongrass of the Potamogetinaceae and *Zannichellia palustris* L., horned-pondweed of the Zanichelliaceae, though usually not marine, are found in brackish waters along the Gulf coasts.

Only two other genera of marine flowering plants are reported from the New World. *Zostera marina* L., eelgrass of the Zosteraceae is found in shallow, quiet waters of the Pacific and Atlantic coasts of North America, reaching as far south along the latter as North Carolina. Other species of this genus have been collected on the coasts of Chili and Uruguay (Setchell, 1934b, 1935). *Phyllospadix scouleri* Hook. and *P. torreyi* Wats., also of the Zosteraceae, grow along the Pacific coast near low-tide mark where they are exposed to strong wave action.

The Gulf and Caribbean sea-grasses are limited in habitat largely to soft marl, mud, or sand in warm, clear, shallow marine water. *Thalassia*, *Diplanthera*, and *Syringodium* form extensive submarine meadows or beds in shallow water of bays and lagoons, seldom being exposed except at the lowest tides. These plants extend also into deeper water, having been dredged in the Dry Tortugas area to 11 meters (Taylor 1928). Generally, the species of *Halophila* thrive on calcareous bottoms in much deeper water. *H. baillonis* has been dredged from 5.5 to 29.3 meters but more commonly in 14 to 18 meters and *H. engelmannii* in still deeper water, 4.6 to 73.2 meters and one estimated depth of 91 meters (Taylor 1928). *H. aschersonii* was dredged with *H. baillonis* along the south shore of Puerto Rico from a depth of 18 meters (Howe 1915). These marine plants are usually associated in southern Florida waters with such marine algae as *Acetabulum*, *Caulerpa*, *Gracilaria*, *Halimeda*, *Hypnea*, *Penicillus*, *Polysiphonia*, *Sargassum*, and *Udotea*. *Thalassia* especially furnishes a good habitat for such algal epiphytes as *Melobesia farinosa* Lamouroux. *Ruppia* is often abundant in shallow water of enclosed bays, tidal estuaries, or other areas where the water is less saline.

The distribution of sea-grasses in the Gulf is poorly known. All five Gulf species grow along the northwestern coast of Cuba and around the Florida Keys. All of these but *H. baillonis* have been collected in the Tampa Bay region by the writer and on the northern Gulf coast of Florida by others. *Thalassia*, *Diplanthera*, and *Halophila engelmanii* are present in the coastal waters of southern Texas. Several of the species must occur along the Mexican coast. The apparent rarity of marine spermatophytes except *Ruppia* on the northern Gulf coast between Bay County, Florida, and Aransas County, Texas, may be significant. Perhaps the silt and fresh water dumped into the Gulf by the Mississippi and other large rivers are involved.

Outside the Gulf and Caribbean, *Diplanthera* has been collected on the coast of North Carolina and *Diplanthera*, *Thalassia*, *Syringodium*, and *H. baillonis* on Bermuda shores. Two species, *Thalassia testudinum* and *Diplanthera wrightii* have been collected on both the Caribbean and Pacific coasts of the Isthmus of Panama, possibly indicating a former water connection across the isthmus. Close relatives of species in each of the four Gulf genera are found in the Indo-Pacific region. In all, approximately 40 species of sea grasses are known, and the largest concentrations of these occur in tropical waters of the Indian Ocean, western Pacific Ocean, and the Red Sea.

MANGROVE SWAMP

Most conspicuous of the plant communities of the Gulf coast is mangrove swamp. There is much literature about this swamp-forest or swamp-thicket that is so characteristic of tropical coasts around the world. Davis (1940) has made a thorough study of mangroves in Florida with emphasis on their ecology and geologic role. Their importance as land-builders in Florida has been emphasized, perhaps overemphasized, by several writers (Curtiss 1888; Sargent 1893; Pollard 1902; Phillips 1903; Vaughan 1910; Harshberger 1914; Simpson 1920). The embryology of *Rhizophora mangle* L. has been studied by Cook (1907), the physiology by Bowman (1917), and the dispersal and establishment by Egler (1948). Dispersal of *Rhizophora* and other mangroves has been considered in some detail by Crossland (1903), Guppy (1906, 1917), Ridley (1930), and other biologists. In addition to some of the above papers good accounts of mangrove swamp on Gulf coasts have been written by Harper (1927) and Davis (1942, 1943). Publications describing

mangrove swamp in other regions are listed in the bibliography for Jamaica (Steers et al. 1940), the Virgin Islands (Børgesen 1909; Raunkiaer 1934), Micronesia (Fosberg 1947), Indo-Malaya (Schimper 1891), and for the tropics in general (Schimper and Faber 1935) and (Warming 1909).

The three widely distributed mangroves of Gulf shores are *Rhizophora mangle* L., the red mangrove, *Avicennia nitida* Jacq., the black or honey mangrove, and *Laguncularia racemosa* (L.) Gaertn. f., the white mangrove. These species grow mixed together or in distinct zones. All are noteworthy for their ability to withstand varying concentrations of salt in the sea water and soil solution in which their roots are buried. They are apparently facultative halophytes, for seedlings of each have been grown in fresh soil and water for at least 6 years (Davis 1943). *Rhizophora* may be readily identified by its peculiar system of branching prop-roots extending downward like stilts from the trunks and lower branches and by the less common flexible air roots dropping from the upper branches. It produces seeds which germinate while attached to the tree to form club-shaped hypocotyls commonly 30 centimeters long. These hang by the two cotyledons from the ovate fruit until they plummet into the water or mud below the tree. *Avicennia* produces an abundance of odd, pencil-like pneumatophores rising through the mud from the shallow horizontal roots. The flowers produce abundant nectar that is manufactured by bees into excellent honey. The fruit is ellipsoid, flattish, and 3 to 5 centimeters long. *Laguncularia* produces fewer and smaller pneumatophores than *Avicennia*. It may be recognized by its fleshy, elliptical leaves and small, ribbed fruit.

In addition to the three mangroves several plants are characteristic of mangrove swamps. A relative of *Laguncularia*, *Conocarpus erecta* L., called the buttonwood or button mangrove because of its small, button-like or alder-like clusters of flowers and fruit, grows inland from the other mangroves on harder ground that is usually not flooded by normal tides. Its trunks are loose-barked, twisted, and frequently prostrate. It is a common plant also in dune hammocks. Two vine-like shrubs of the Leguminosae, *Caesalpinia crista* L., nicker-bean, and *Dalbergia ecastophyllum* L., coin-vine, often sprawl over the mangrove thickets on their landward margin. Both species are more shrub-like when growing on the dunes. Another vine, of the grape family, *Cissus incisa* (Nutt.) Desmoul., marine-ivy, climbs through the crowns of the mangroves and sends down to the ground long, cord-like aerial roots. *Batis maritima* L., saltwort, a succulent-leaved, spreading or prostrate shrub, is frequently the only species accompanying the mangroves on wet mud. On sandy or marly shores other succulent halophytes, such as *Salicornia virginica* L., glasswort, *Sesuvium portulacastrum* L., sea-purslane, and *Suaeda linearis* (Ell.) Moq., sea-blite, and several grasses may cover the ground on the inner margin of the mangrove thickets.

On drier ground landward from the mangrove thickets several shrubs and herbs associated with *Conocarpus* form an open thicket transitional to shore hammock or pineland. Some of the plants of this transitional zone, flooded by salt water only during spring and storm tides, are *Borrichia frutescens* (L.) DC., sea-oxeye, *Lycium carolinianum* Walt., Christmasberry, *Bumelia celastrina* HBK., saffron-plum, *Coccoloba uvifera* (L.) Jacq., sea-grape, *Maytenus phyllanthoides* Benth., and *Sophora tomentosa* L., necklace-pod. In addition to these, all found in the Tampa Bay region of central Florida, several other tropical associates of *Conocarpus* in the mangrove-hammock transition zone are found in the more tropical part of southern Florida and the Florida Keys. These are *Borrichia arborescens* (L.) DC., sea-oxeye, *Rhabdadenia biflora* (Jacq.) Muell. Arg., rubbervine, *Capparis flexuosa* L., *Achras emarginata* (L.) Little, wild dilly, *Jacquinia keyensis* Mez., Joewood, *Torrubia longifolia* (Heimerl.) Britt., blolly, *Erythalis fruticosa* L., *Acrostichum aureum* L., leather fern, and several cacti, *Acanthocereus floridanus* Small, dildoe, *Harrisia simpsonii* Small, prickly-apple, and *Opuntia dillenii* (Ker) Haw, prickly-pear. The loose bark of *Conocarpus* furnishes a foothold to several epiphytes including *Epidendrum tampense* Lindl., an orchid, and various species of *Tillandsia*, the air-pines.

Zonation in mangrove swamps appears to be correlated with water level and degree of salinity of the water and substrate and in some areas with tidal fluctuations. Each species, however, may be quite variable in relation to these factors. *Rhizophora* may form colonies well off shore on

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shoals or may occur as scattered plants in brackish or even fresh water well inland from the coast. Generally, it grows on shores or low islands where the substrate is covered by tidal water even at low tide. The *Avicennia* zone which commonly includes *Laguncularia* and various salt-marsh plants is flooded, at least in its outer part, by salt or brackish water at high tide. When *Laguncularia* forms a distinct community, it is usually inland from *Avicennia*. *Conocarpus* and its associates of the transition zone are seldom flooded. The mangroves grow on peat, muck, marl, sand, and rock. They are killed by severe frosts. Economically they have been of little importance except in certain areas where they have been used for fuel, pilings, and a source of tannin. It is contended by some that mangrove swamps protect shorelines, build up soil levels along the coast, extend shorelines, and form new islands, but it is doubtful that the mangroves play a very large part in land building.

Mangrove swamp in the Gulf region reaches its greatest development along the southwestern coast of Florida in the Ten Thousand Islands area. There mangroves of all three species, some more than 25 meters tall and 2 meters in circumference (Davis 1940), grow in the extensive strand and estuary swamps. Mangrove swamp to a depth of several miles covers the western and southern tip of peninsular Florida from Cape Romano to Cape Sable and thence eastward to Biscayne Bay. Mangroves also cover the numerous small keys in Florida Bay and fringe the larger Florida Keys south and west to the Marquesas. Northward along both sides of Florida less well developed mangrove swamp, perhaps better described as mangrove thicket, extends to the Cedar Keys area on the Gulf coast and Cape Canaveral or farther north on the Atlantic coast, mostly in lagoons, bays, and estuaries. As the mangroves become smaller and more scattered on the northern Gulf coast, salt marshes become more extensive. Killing frosts apparently are the deciding factor in the competition between the species comprising the two vegetation types. In Florida mangrove areas are estimated to total more than a thousand square miles (Davis 1940).

The botanically less known Gulf coasts of Cuba and Mexico are fringed in the appropriate habitats with mangrove swamp. According to Leopold (1950), mangroves extend northward along the Mexican Gulf coast to southern Tamaulipas. Along the northern shores of the Gulf from Cedar Keys in Florida to southern Tamaulipas typical mangrove swamp is absent, and mangrove species are represented only by the more hardy *Avicennia* which grows, where present, mostly as scattered shrubs with *Batis* and other salt-marsh associates.

Mangrove swamp is found throughout the tropics along low-lying shores and estuaries that are protected from direct wave action. Although it is best developed on mud and marl, it is present also on sand and even rock wherever crevices permit the seedling mangroves to gain a foothold (Crossland 1903). Oriental mangrove swamps are similar to those of the American and West African shores except that there are many more species of Oriental mangroves. Although few in number the American mangroves are widely distributed. *Rhizophora mangle*, *Avicennia nitida*, and *Laguncularia racemosa* are all found on the tropical coasts of West Africa as well as on both Pacific and Atlantic shores of tropical America. The floating seedlings or fruits of all three remain buoyant and alive in salt water for several months (Guppy 1917) and are thus well-adapted to long distance dispersal by ocean currents. Several of the plants associated with them on the Gulf coasts, such as *Caesalpinia crista*, *Sophora tomentosa*, and *Acrostichum aureum*, range even more widely in the tropics.

SALT MARSH

Salt marshes of temperate shores have received perhaps even more attention from botanists than mangrove swamps of tropical shores. Those along the Gulf coast have not been neglected. Penfound and Hathaway (1938) have made a very thorough study of marshes in southern Louisiana. Other botanists who have published on salt marshes of the northern Gulf shores are Mohr (1901), Lloyd and Tracy (1901), Cook (1907), and Penfound and O'Neill (1934). Harshberger (1914), Harper (1927), and Davis (1940, 1943) have described salt marshes and salt flats along the Florida Gulf coast. The salt marshes along the Atlantic coast of North America are similar in many respects, and have been well described by Kearney (1900, 1901), Harshberger (1909), Johnson and York (1915), Conard (1935), and Chapman (1940a, 1940b).

Salt marshes are best developed along the more protected, temperate shores of the northern part of the Gulf of Mexico. There extensive marshes of salt-tolerating species of flowering plants cover the tidal shores of the estuaries, bays, and lagoons. According to Griffitts (1928) there are 5,600,000 acres of salt marshes in the South Atlantic and Gulf States, of which 3,381,500 are in Louisiana, 680,000 in Florida, 315,000 in Texas, 34,000 in Alabama, and 26,500 in Mississippi. Louisiana possesses almost one-half of the total salt-marsh acreage in the United States.

The dominant species in these marshes are *Spartina alterniflora* Loisel., smooth cordgrass, and *Juncus roemerianus* Scheele, black rush, each commonly forming extensive and exclusive colonies. Several other grasses or grasslike plants, however, are often found in association with them. These are *Distichlis spicata* (L.) Greene, saltgrass, *Spartina patens* (Ait.) Muhl., salt-meadow cordgrass, *Spartina spartinae* (Trin.) Merr., *Scirpus robustus* Pursh, salt-marsh bulrush, and *Fimbristylis castanea* (Michx.) Vahl, a sedge. Showy-flowered plants like *Limonium carolinianum* (Walt.) Britt., sea-rosemary, *Solidago sempervirens* L. var. *mexicana* (L.) Fern., seaside goldenrod, *Pluchea purpurascens* (Sw.) DC., salt-marsh fleabane, *Aster exilis* Ell., *A. subulatus* Michx., and *A. tenuifolius* L., the salt-marsh asters, and *Borrichia frutescens* (L.) DC., sea-oxeye, give some color to the marshes though they are seldom abundant.

On wet, saline flat areas which are near high tide-mark the vegetation is more open. There, sometimes with scattered and dwarfed specimens of *Avicennia nitida* L., black mangrove, and several plants, such as *Distichlis*, *Borrichia*, and *Limonium*, are found the peculiar halophytes with succulent stems or leaves, *Batis maritima* L., saltwort, *Salicornia virginica* L. and *S. bigelovii* Torr., glassworts, *Suaeda linearis* (Ell.) Moq., sea-blite, *Sesuvium portulacastrum* L., sea-purslane *Philoxerus vermicularis* (L.) R. Br., beach-carpet, and *Bacopa monnieri* (L.) Pennell, marsh-hyssop. With these grow a few species with showier flowers: *Sabatia stellaris* Pursh, sea-pink, *Gerardia maritima* Raf., false-foxglove, and two vines, *Ipomoea sagittata* Cav. and *Cynanchum palustre* (Pursh) Heller. On slightly higher ground these herbs or small shrubs give way to a thicket of taller shrubs consisting mostly of *Iva frutescens* L., marsh-elder, *Baccharis halimifolia* L. and *B. angustifolia* Michx., groundselbushes.

Farther south along the Florida Gulf coast from Tampa Bay to Key West the salt marshes become much less extensive due to competition from the mangroves. Salt-marsh plants there generally form an understory in the *Avicennia* zone of the mangrove swamps or predominate in the transition zone between the mangroves and non-halophytic vegetation. Characteristic of this southern Florida coast, especially on Cape Sable, are the salt flats. These level expanses of hard-packed sand or marl or of limestone rock are flooded by high tides. They support a sparse vegetation of species listed above for the open salt marsh with the addition of several other common plants like *Monanthochlöe littoralis* Engelm., key grass, *Sporobolus virginicus* (L.) Kunth, drop-seed, *Borrichia arborescens* (L.) DC., sea-oxeye, *Flaveria linearis* Lag., *Conocarpus erecta* L., buttonwood, and its other woody associates listed under mangrove swamps.

In the marshlands of southeastern Louisiana Penfound and Hathaway (1938) found gradual changes in the flora from strictly salt-water to strictly fresh-water habitats. They noted that many marsh species have a wide range of tolerance for the salt factor and are found in brackish marshes as well as in salt-water or fresh-water marshes. Most of the salt-marsh species listed previously occur also in brackish water, and many fresh-water marsh plants are found in slightly brackish water. Some of these plants of brackish marshes are *Typha domingensis* Pers. and *T. latifolia* L., cattails, *Spartina cynosuroides* (L.) Roth, salt-reed grass, *Phragmites communis*, Trin., common reed, *Scirpus californicus* (C. A. Meyer) Britt. and *S. chilensis* Nees & Mey., bulrushes, *Sagittaria lancifolia* L., arrowhead, and *Alternanthera philoxeroides* (Mart.) Griseb., alligator-weed. The last-mentioned plant is often a pest in the bayous and ditches of southern Louisiana. Another bad pest of fresh waters, *Eichornia crassipes* (Mart.) Solms, water-hyacinth, although often floated downstream into salt water, will not tolerate salt, and soon dies in even slightly brackish water (Penfound and Earle 1948).

In southern Florida the transition from salt marsh or mangrove swamp to nonhalophytic types of vegetation is equally gradual or very abrupt. Where salt marsh is transitional between man-

grove swamp and fresh-water prairie the brackish marsh zone is very wide. Dwarfed and scattered specimens of *Rhizophora mangle* L. grow inland along the rivers running from the Everglades and in the wet prairies where the water has little or no salt content. There it may be associated with *Cladium jamaicensis* Crantz, sawgrass, *Typha domingensis* Pers., cattail, *Sagittaria lancifolia* L., arrowhead, *Acrostichum danaeaefolium* Langsd. & Fisch., leather fern, and *Annona glabra* L., custard-apple. Similarly, where large rivers flow into the Gulf there are along the estuaries wide areas of brackish marshes transitional between the coastal salt marshes and fresh-water marshes and swamps. Where salt marsh abuts upon pineland, as in the Tampa Bay region, a difference of 30 centimeters in ground level brings an abrupt change in the physiognomy of the vegetation. The narrow zone of transition is often marked by a thicket of *Myrica cerifera* L., waxmyrtle, several species of *Baccharis*, groundselbushes, and *Sabal palmetto* (Walt.) Todd., cabbage palm.

There are no salt marshes on the Cuban Gulf coast. Many of the American salt-marsh species, however, grow mixed with tropical species in the mangrove swamps or on low-lying beaches. Although the coastal vegetation of Mexico is poorly known, the same relationship probably exists between salt-marsh plants and mangroves from southern Tamaulipas to Yucatán as on the southern Gulf coast of Florida and Cuba. The Yucatán coast possesses such salt-marsh or salt-flat plants as *Distichlis*, *Monanthochlöe*, *Spartina*, *Sporobolus*, *Fimbristylis*, *Philoxerus*, *Salicornia*, *Suaeda*, *Batis*, *Sesuvium*, *Baccharis*, and *Borrichia*, as well as the mangroves and many associated plants.

Salt-marsh plants live under most difficult conditions: high salt content in the soil solution, poor aeration resulting from the poor drainage, recurrent submersion and exposure, and full insolation. Only species with a wide range of tolerance to these conditions can survive. Marsh height, tidal submergence, and salinity of the soil solution appear to be the most important factors in producing zonation in salt marshes. *Spartina alterniflora* Loisel. withstands the deepest flooding. It is also, with *Distichlis spicata*, *Juncus roemerianus*, *Batis*, *Salicornia*, and the other succulent halophytes, apparently the most salt-resistant. Uphof (1941) has reviewed the literature on halophytes.

SAND-STRAND VEGETATION

The flowering plants of sandy shores are not strictly aquatic, yet they are too conspicuous and too abundant along Gulf coasts to omit from this treatment. Most thoroughly studied and described are the Florida beaches. Webber (1898), Millspaugh (1907), Harshberger (1914), Bowman (1918), Simpson (1920), Harper (1927), Davis (1940, 1942, 1943), and Kurz (1942) have described the beach vegetation of the Florida Gulf coast. Strand vegetation along the northern Gulf coast has been treated by Mohr (1901), Lloyd and Tracy (1901), Cocks (1907), Lowe (1921), and Penfound and O'Neill (1934). Except for the addition of more tropical species and the dropping out of more temperate species, the strand flora of Yucatán, Cuba, and other West Indian islands is very similar to that of southern Florida. This similarity is readily apparent from the descriptions of the beach vegetation of Yucatán (Bequaert 1933; Lundell 1934), Cuba (Uphof 1924; Seifriz 1943), Puerto Rico (Cook and Gleason 1928), and the Virgin Islands (Børgesen 1909; Raunkiaer, 1934). Beach and dune vegetation along the Atlantic Coast of North America is described by Kearney (1900, 1901), Harshberger (1900), and Conard (1935). General treatments of strand vegetation in other parts of the world can be found in Schimper (1891), Schimper and Faber (1935), and Warming (1909).

Sandy shores of the Gulf coast show as definite a zonation as salt marshes and mangrove swamps. Oosting (1945) attributes this zonation to the tolerance to salt spray of the various coastal dune plants. The community is definitely a halophytic one. Due to vigorous wave action few plants survive on the lower beach. The pioneers of wet or shifting saline sands are found on the upper beach and the fore dunes. In the Tampa Bay region of the Florida coast the most abundant strand species are *Sesuvium portulacastrum* L., sea-purslane, *Sporobolus virginicus* (L.) Kunth, drop-seed, *Atriplex arenaria* Nutt., beach orach, *Cakile edentula* (Bigel.) Hook., sea-rocket, *Heliotropium curassavicum* L., seaside heliotrope, *Philoxerus vermicularis* (L.) R. Br., beach-carpet, *Iva imbricata* Walt., beach-elder, *Uniola paniculata* L., sea-oats, *Euphorbia buxifolia* Lam. and *E. ammannioides* HBK., spurges, *Ipomoea pes-caprae* (L.) Sweet and *I. littoralis* (L.) Boiss.,

railroad vines, *Scaevola plumieri* Vahl, beach berry, *Andropogon glomeratus* (Walt.) BSP., bunchgrass, *Cenchrus pauciflorus* Benth., sandbur, *Croton punctatus* Jacq., silverleaf, *Oenothera humifusa* Nutt., seaside evening-primrose, and *Helianthus debilis* Nutt., dune sunflower.

Many of these species, especially the dominant, graceful sea-oats, *Uniola*, remain abundant in the back dunes and dune plateaus inland from the beach. Here, however, the conspicuous species are the larger plants like *Coccoloba uvifera* (L.) Jacq., the seagrape, which is the most characteristic shrub of sandy strands in the American tropics. Other woody species are *Yucca aloifolia* L., Spanish-bayonet, *Forestiera porulosa* (Michx.) Poir., Florida privet, *Chiococca alba* (L.) A. Hitchc., snowberry, *Ernodea littoralis* Sw., *Myrica cerifera* L., waxmyrtle, *Sabal palmetto* (Walt.) Todd., cabbage palm, *Suriana maritima* L., bay-cedar, *Lantana ovatifolia* Britt., shrub-verbena, *Sophora tomentosa* L., necklace-pod, *Dalbergia ecastophyllum* L., coin-vine, *Canavalia obtusifolia* (Lam.) DC., bay bean, *Zanthoxylum clava-herculis* L., toothache tree, *Rapanea guianensis* Aubl., myrsine, *Ardisia escallonioides* Schlecht. & Cham., marlberry, and *Eugenia axillaris* (Sw.) Willd., white stopper. Most of these beaches and dunes along the central Florida coast are on narrow barrier islands which are covered with strand vegetation on the Gulf side and mangrove thicket on the bay side. Between these two types of vegetation may be developed a grassy palm savannah with *Sabal* dominant or a dense coastal hammock composed of more luxuriant and crowded growth of the same species listed above for the back dunes.

Along the northern Gulf coast many of the tropical elements of the dunes and dune-plateau drop out. On the other hand, some of the temperate species are replaced by more tropical species on the Florida Keys and northwestern coast of Cuba. Among the more important additions to the strand flora there are *Tournefortia gnaphalodes* (Jacq.) R. Br., sea-lavender, *Casasia clusiifolia* (Jacq.) Urban, seven-year-apple, *Erithalis fruticosa* L., *Strumpfia maritima* Jacq., *Chrysobalanus icaco* L., coco-plum, and the less common, poisonous *Hippomane mancinella* L., manchineel. Most of the strand species are widely distributed throughout the tropics, and a few, like *Ipomoea pes-caprae* (L.) Sweet are circumtropical. One exotic tree from Oceanica, *Casuarina equisetifolia* Forst., Australian-pine or beefwood, has become widely naturalized on the sandy shores of peninsular Florida and the West Indies. On some of the Florida beaches it is the dominant tree.

Most of the abundant species of the Florida and Cuba beaches and dunes are listed from Yucatán, and the strand vegetation along the rest of the Mexican Gulf coast is probably similar to that of the southeastern shores of the Gulf. Little seems to have been published on the vegetation of the Texas coast, but there, too, the strand flora must be rather similar to that of the Florida coast in the same latitude.

CONCLUSION

The vegetation of the shallow waters and shores of the Gulf of Mexico includes four principal communities of flowering plants. Throughout the Gulf a characteristic strand flora grows on exposed sandy shores of the fringing barrier islands, the larger bays, and the headlands. Grass-like marine spermatophytes form submarine meadows or carpets in shallow, quiet waters, except along the extreme northern Gulf coast. Extensive salt marshes cover muddy, protected shores in lagoons, bays, and estuaries along the northern Gulf coasts. Protected shores in the central and southern Gulf region, however, support swamps or thickets dominated by mangroves, with salt-marsh plants restricted to small areas of open marsh, to open saline flats, or to the understory of the more open zones of the mangrove swamps.

Knowledge of the flora and vegetation of most of the Gulf shores is relatively meager. Only the coast from Louisiana to the Florida Keys has received considerable attention from botanists. The Cuban and Texan coasts have largely been neglected, and the Mexican coast, excluding Yucatán, has received almost no botanical attention. The whole Gulf perimeter should be subjected to an intensive, systematic survey by competent plant taxonomists and ecologists.

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BOTTOM COMMUNITIES OF THE GULF OF MEXICO

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The study of bottom communities, according to the quantitative approach of Petersen, has not been attempted in the Gulf of Mexico or its coastal bays. It is possible to assemble information, in a general way, about certain characteristic bottom aggregations such as coral reefs, sponge grounds, and oyster beds, but the necessary data for comparing these areas with similar situations elsewhere do not exist. This gap in our knowledge has been due in part to our fragmentary information concerning the qualitative composition of the flora and fauna of the area. As many of the contributors of the sections on various animal groups in this volume have shown, our knowledge of the fauna is still far from satisfactory. It is, on the other hand, not without advantage that we have lagged behind other countries in quantitative bottom studies, since we may profit by example. Leaders in this field in recent years have been Russian fishery biologists whose work on biological productivity, biomass, and bottom communities in general has been summarized up to 1947 by Zenkevich (1947). Discussion of the methods and principles of this work are available in English (Brotskaja and Zenkevich, 1939; Zenkevich and Brotzky, 1939). It must be pointed out that such concepts of "productivity," "production," and "biomass" should be used with caution and only after careful consideration of the life spans and metabolic rates of the components of the community.

An example of a study of sponge grounds, in some ways comparable to those off western Florida, will be found in the paper by Chambost (1928). Communities of bay bottoms, including many closely related species living under similar conditions to those encountered along the northern Gulf coast, have been recently described by de Oliveira (1948, 1950). The literature on North Atlantic bottom communities has been reviewed by Jones (1950) who also discusses the concept of marine communities in general.

There is a certain amount of published misinformation, most of it well intentioned, concerning the occurrence of organisms which are considered important community dominants in the Gulf of Mexico. Andree (1920, v. 2, pl. 7), for example, presents a map indicating the occurrence of pearl oysters from Panama northward to Texas and eastward to Alabama. Literally, this is true; small specimens of *Pinctada* are frequently cast adrift on sargassum and reach these coasts, but there are no pearling grounds in the northern Gulf. At the same time, however, reef building oysters are not indicated west of the Atlantic side of Florida, and there is no indication of the Gulf of Mexico sponge grounds. This is comparable to the gaps in Bartholomew's (1911) Atlas of Zoogeography and Orton's (1937) peculiar omission of oysters from the northern Gulf coast. The well-known map of coral reefs indicating reefs throughout the Gulf prepared many years ago by Joubin has appeared in many texts (including the standard Russian text on hydrography). From such information as this, Ekman (1935) originally classified the northern Gulf of Mexico as a tropical littoral region. In his new edition Ekman (1953) gives a more precise account, characterizing the northern part of the Gulf of Mexico as a "warm temperate" region, with species common to temperate eastern North America. A more detailed discussion of the biogeographical relationships of the northern Gulf of Mexico will be found in Hedgpeth (1953).

Of the various bottom communities in the Gulf of Mexico, several of them of prime economic importance, the most intensive work has been done on the oyster bottoms. Various surveys have been undertaken, mostly with the purpose of delineating the beds and determining the causes of decline. While most of the published surveys are out of date, they are useful in studying the changes, many of them the result of human interference with the environment, which have

occurred subsequently. The results of the most recent and intensive surveys are not generally available, although two minor papers from one of them have appeared (Norris 1953; Puffer and Emerson 1953).

Most of the study of coral reefs has been faunistic or geological; some minor contributions to the ecology of Gulf of Mexico coral reefs are to be found in the publications of the Tortugas Laboratory. The sponge grounds have been even less adequately studied from the ecological standpoint, although investigations are now in progress.

Gunter's work in Louisiana and Texas

Important marine ecological work, chiefly with motile invertebrates and bottom-feeding fishes, has been done by Gunter in the past 20 years on the coast of Louisiana and Texas. The general results can be divided into the following main categories:

1. A description of the relative abundance and species mass of the larger motile vertebrates and invertebrates.

2. Description of seasonal cycles and movements from Gulf to estuarine waters and return, and seasonal variations in abundance, correlated with temperature change.

3. Distributions of organisms as related to salinity.

This work probably gives as complete a view of the motile and free-swimming fauna of the bays and shallow Gulf as there is for any coast of this continent. While it describes the motile part of the bottom community it does not add to knowledge of the in-fauna of the bottoms. Life history notes on the various important fish and Crustacea with some data on food consumption were gathered as a side issue.

The work in Louisiana was carried on for 2 years from 1931 to 1933. It consisted of the analysis of populations of bottom fishes over a salinity gradient from almost fresh water in the upper part of Barataria Bay to 3 miles offshore in the open Gulf of Mexico. It was during this initial work that Gunter became interested in relative numbers of species mass which he emphasized in later papers. In view of the impossibility of obtaining knowledge of total quantities of the species involved, the relative numbers data of the animals taken in the various environments seem to be about as quantitative as can be obtained. This was used in estimating the relative species mass. Any gear used gives a somewhat distorted view of the actual populations, and the various advantages and disadvantages of the trawl were considered. The results of this work were given in Gunter (1936, 1938a, b). The seasonal variations in abundance of the whole fish population and of various species alone are given. The seasonal cycle of movement in and out of the bays, giving somewhat regular arrivals and departures of some species, was described. The predominant family of fishes was found to be Sciaenidae, followed by Otolithidae and Engraulidae. Several abundant species of Sciaenidae were led by the croaker, *Micropogon undulatus*. Certain comparisons between the shallow water fish fauna of the Louisiana and Texas coasts were made later (Gunter 1945). This work was done under the auspices of Shrimp Investigations of the United States Bureau of Fisheries, and during this time large catches of shrimp were made. The data have not been published, but it can be said that the motile fauna living close to the bottom in the Louisiana bays and shallow Gulf consists chiefly of the fishes described by Gunter, the peneid shrimp, *Penaeus setiferus* and *Penaeus aztecus*, and the blue crab, *Callinectes sapidus*.

During the years 1941 to 1943 Gunter set up a series of stations covering a transect from almost pure fresh water (salinity 2.1 parts per thousand) to 5 miles offshore in the Gulf of Mexico and 5 miles down the Gulf beach. This was on the Texas coast and ran through Copano Bay and Aransas Bay and out into the Gulf, a distance of 40 nautical miles. Thirty-two stations were covered by trawl hauls, trammel nets, beach seines, and fine-mesh net hauls on the beach and shores. The original plan was to carry the work on for 2 years, but it was carried out for a year and a half, and only 1 full year without spotty collections was obtained. Even so, it covered bay and estuarine waters and the connecting sea as extensively as has been done in this country.

Gunter (1945, 1950) was considerably impressed with the fact that the bays serve as nursery grounds for large numbers of organisms. For instance, many fishes such as the croaker, *Micropogon undulatus*, the redfish, *Sciaenops ocellata*, the mullet, *Mugil cephalus*, and several others spawn in the Gulf and grow up in the bays. The same holds true for the blue crab, *Callinectes*

sapidus, and the two shrimp, *Penaeus setiferus* and *P. aztecus*, all important components of the fauna. This system of bay waters forms a rim along the whole northern Gulf coast. Although certain species such as the cyprinodont fishes, the common oyster, and the various species of palaemonid shrimp remain in the bays and are found nowhere else, the bays are not faunistically isolated from the shallow Gulf, despite narrow connections through the passes, but form a system with it. The dominant life of the region has perforce become adapted to this estuarine-sea water system and moves back and forth within it during the life cycle.

Gunter also emphasized the importance of two gradients connected or correlated with salinity. One, an ostensible relation between salinity and size, depends on the fact that most motile animals move out from shallower waters as they grow larger and go toward or to the sea. This migration is accelerated by the onset of cool weather in the fall when large movements from the bays to the Gulf take place amounting almost to a general exodus for some species.

The other gradient is a decline in the number of species as the salinity falls. As he pointed out, the bay fauna is marine, and although practically all species can live in high salinities they only tolerate varying degrees of low salinity, and thus the numbers of species present become less as the salinity falls along the gradient. The difference in numbers of species in the Gulf and Copano Bay is particularly striking in winter. At that season the fresher, shallower, and thus cooler waters of Copano Bay are dominated by only four or five motile species. The importance of these general phenomena to paleoecological studies was specially mentioned (Gunter 1947).

Since ecological studies by Gunter did not include the sessile, poorly motile or burrowing forms in the area they are incomplete. Nevertheless, they go a long way toward describing the communities of the shallow Gulf. Readers interested in details should consult the original papers. As for the deeper water communities, virtually nothing is known except the results of sporadic dredging stations by the *Blake* and *Albatross* more than 50 years ago. There has been no attempt to list the findings of these dredgings by stations, a difficult task of reassembling in view of the scattered publication of reports on the various animal groups. Hence, our knowledge of the deep-water life of the Gulf of Mexico is still that of Agassiz' Three Cruises of the *Blake*.

Investigations of recent facies

A relatively new development is the study of assemblages of living (and dead) organisms as potential fossil assemblages. In such studies, groupings or facies correlated with environmental conditions are emphasized. Such facies may be the same as a natural community (especially that of the oyster reefs), or they may have no particular relationship to the communities in which they occur especially if they include such remains as mollusk shells and coral fragments carried there by physical forces. In his study of molluscan-foraminiferan assemblages in San Antonio and Aransas Bays, Texas, Ladd (1951) recognizes a series of facies roughly corresponding to the salinity gradient: bay head, inter-reef, reef, polyhaline bay, passes, open gulf (near- and offshore), beaches, and highly saline lagoon. A similar series, based exclusively on foraminifera is recognized in the same region by Parker, Phleger, and Peirson (1953); river, marsh, bay, beach and open gulf. The distribution of various foraminifera along several transects in the northern Gulf from Florida to Texas in relation to sedimentary facies is discussed by Lowman (1949).

Community terminology

The matter of terminology and classification of marine communities, in general, is not settled. The ambitious attempt of Clements and Shelford (1939) to classify the biota of the North Atlantic into various biomes and their component associations has served principally to emphasize that the criteria of terrestrial biomes have but limited application to the marine environment. The term biome was accepted somewhat uncritically by Jones (1950) who classified the North Atlantic bottom communities into various hard and soft bottom "biomes." It is suggested in the recent monumental treatise of Allee et al. (1949), that self-sustaining communities within the sea are difficult to recognize, and that biomes, as defined on land, do not exist: "The major marine community despite its great regional biotic variation, is so lacking in effective barriers to dispersal, is so much subject to slow continuous circulation of its medium and exhibits so much interdepend-

ence of its components from region to region and area to area, that it may be regarded as a single biome type." This is probably an extreme view, but in view of our ignorance concerning the bottom communities of the Gulf of Mexico, we cannot examine this question in detail here.

It is necessary to emphasize, however, that the complex character of marine communities cannot be simplified by terminology. The dual character of that community which includes the various species of shrimp is an example. Both estuarine and neritic bottom communities are part of this complex which may be best regarded as elements in a major ecosystem transgressing the various environments in both space and time (Hedgpeth 1953). For the purposes of discussion, several "major bottom communities" are recognized (fig. 51). The four major communities recognized are: the oyster bottoms, the shrimp grounds, the coral reefs and patches, and the sponge grounds. The sponge grounds occupy roughly the same area as the coral patches west of Florida and may, on further study, be considered a subcommunity of the coral grounds. Segregating these by physiographic or environmental requirements, we have in the euryhaline-bay environment the oyster community (and other communities); the shrimping grounds fall in the estuarine and neritic environment; while the coral and sponge communities are stenohaline-neritic. These are also working labels, simply describing as briefly as possible the conditions in which the communities are found.

THE OYSTER COMMUNITY

Foremost among the communities of bay waters is the oyster community. This is not a continuous

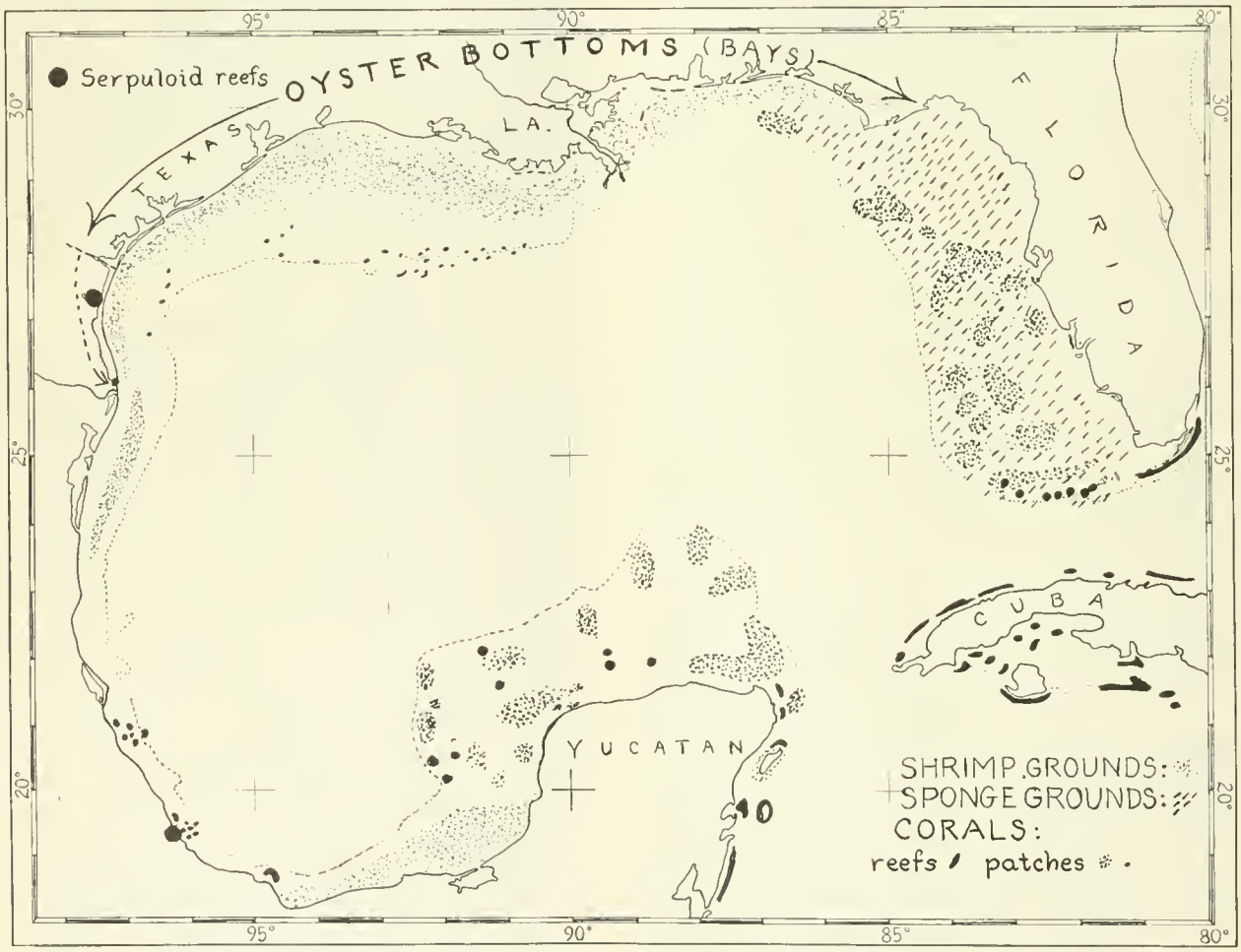

FIGURE 51.—Approximate location of major bottom communities in the Gulf of Mexico.

aggregation of oysters covering entire bay bottoms but an arrangement of ridges and patches of oysters and dead shells, "fragmented faciations of the *Macoma-Mya* biome," in the language of Clements and Shelford (1939). Since *Mya* is absent from Gulf waters and *Macoma* sparsely scattered, this terminology has little meaning. To think of oyster reefs as isolated patches in extensive clam beds is to overlook the influence of oysters in changing the bottom of the bays and the conditions of life for the clams. The clam beds, where they may occur, might better be considered as fragmented by the oyster reefs.

The formation of oyster reefs was studied by Grave (1905) who proposed a theory of the formation of oyster reefs transversely across bays. This theory still remains the best explanation for this characteristic placing of oyster reefs. See figure 52 for a sampling of typical examples, including some studied by Grave.[1] As may be seen from the figure, not all reefs are transverse; some are parallel to the main currents.

The typical oyster reef on the Gulf coast is, in cross section, a low mound with a high center, or "hogback," which is occupied by loose dead shells with the live oysters on the sloping shoulders. These reefs occur on muddy bottoms widely distributed in bays of lower salinities and more or less restricted to the upper ends of those bays which are subject to the invasion of higher salinities through the passes from the Gulf during periods of low rainfall and decreased run-off. A natural reef is usually oval or spindle-shaped or is a narrow bar extending from the shore. Although reefs in Texas have been badly cut up in recent years by artificial channels and mudshell dredging so that the original pattern is now obscured, the usual location of the reefs is such that their long axes are at right angles to the prevailing currents of the bays. Many of these reefs can be studied in the various coastal charts, and details of the more important oyster reefs of the Gulf waters will be found in the old survey papers of Cary (1906), Galtsoff (1931), Moore (1899, 1907, 1913a, 1913b), Moore and Danglade (1915). Ecological accounts will be found in Pearse and Wharton (1938), Archer (1947, 1948a, 1948b), Puffer and Emerson (1953, pp. 164–173).

[1] The biology of the oyster of the Gulf coast and the oyster reefs of the Gulf of Mexico are discussed in detail in chapter XV of this book in articles by Philip A. Butler, p. 479, and W. Armstrong Price, p. 491.

Gulf coast oyster communities differ from those of Chesapeake Bay and more northern waters in lacking predacious starfish, and the Atlantic oyster drill, *Urosalpinx*, is replaced in the lower bays of the Gulf by *Thais*. Other than this, the communities are essentially like those of the Atlantic coast. One of the peculiarities of distribution within the oyster community or biocoenosis is the apparent absence of the commensal (or at times parasitic) crab, *Pinnotheres ostreum*, from the northeastern part of the Gulf, although it has been reported from Cameron, Louisiana, and is not rare in Matagorda and Mesquite Bays in Texas.

There are some examples of marginal oyster communities which are worthy of notice. In parts of coastal Louisiana, especially in the vicinity of Atchafalaya Bay and Marsh Island, oyster reefs in the bays have been reduced by invasion of fresh water, and salinity conditions suitable for the development of reefs are found in the Gulf itself. At the other extreme, a small oyster community persists near Port Isabel where salinities are nearly oceanic most of the year, and the epifauna is characteristically marine (Hedgpeth 1953).

Since the reefs south of Marsh Island were mapped in 1906 by Cary, there seems to have been little change in their extent, and they remain the only extensive oyster reefs known in the Gulf of Mexico proper. From time to time there have been rumors of large reefs in offshore waters, but these rumors seem to be kin to those of fabulous lost mines which can never be found.

Clam beds have been reported for various places, but none have been studied. The low-salinity *Rangia* forms extensive beds in Louisiana and brackish lakes of Texas as far south as Green Lake. Extensive worm communities probably exist, in view of the great shrimp populations, but none have been studied in detail. We have only recently begun to learn which species of worms occur (Hartman 1951). Beds of *Spiochaetopterus* have been observed in Louisiana. The only study of clam beds is that of Spaulding (1906) who worked out the distribution of clams and scallops in the Chandeleur Islands (fig. 53).

Investigations of bottom communities in Texas and Louisiana are now being conducted as part of a study of the nearshore Recent sediments. This project is sponsored by the American Petroleum Institute (Shepard and Moody, 1952). The

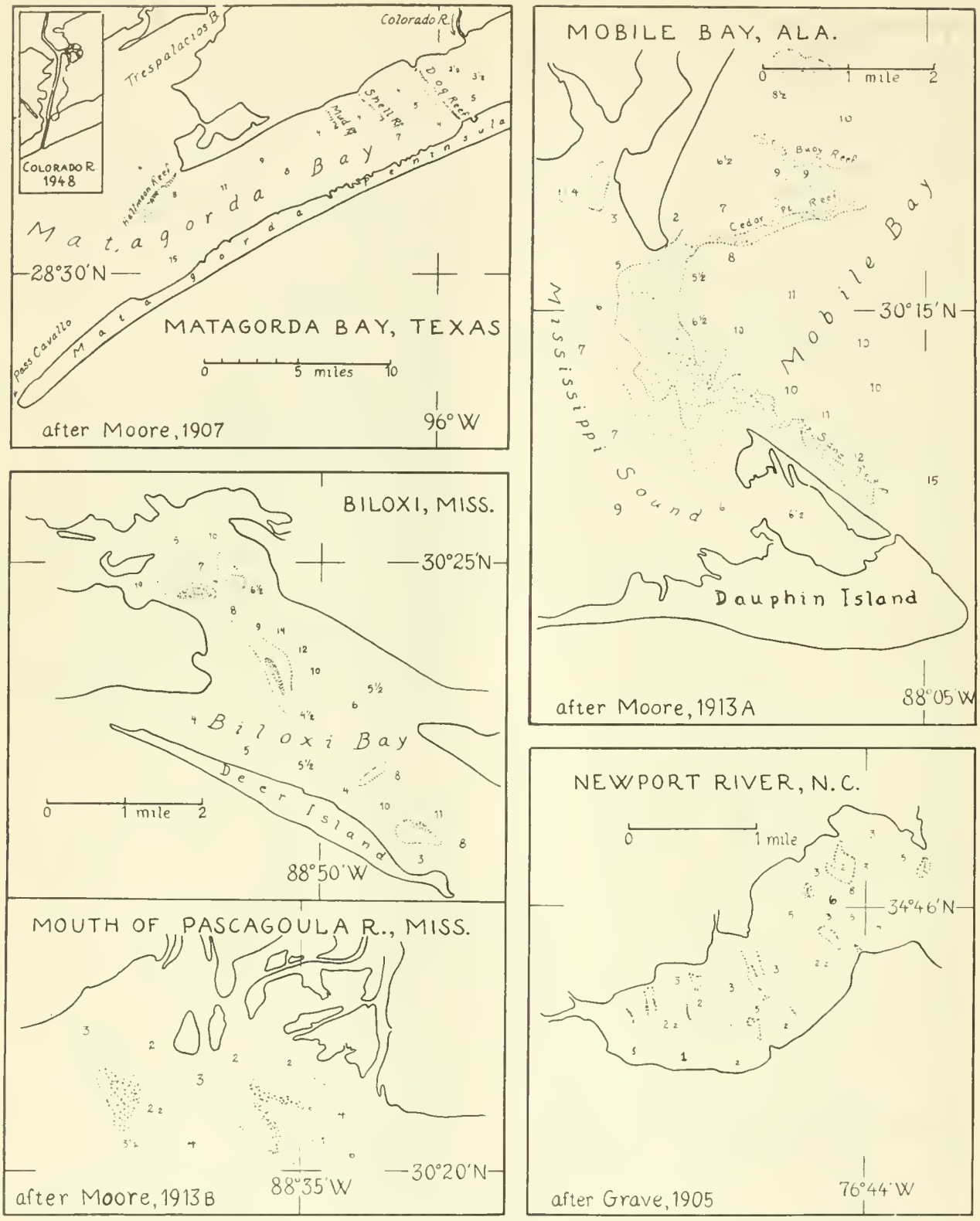

FIGURE 52.—Characteristic Gulf coast oyster reefs from various survey reports as indicated, together with those of Newport River, North Carolina.

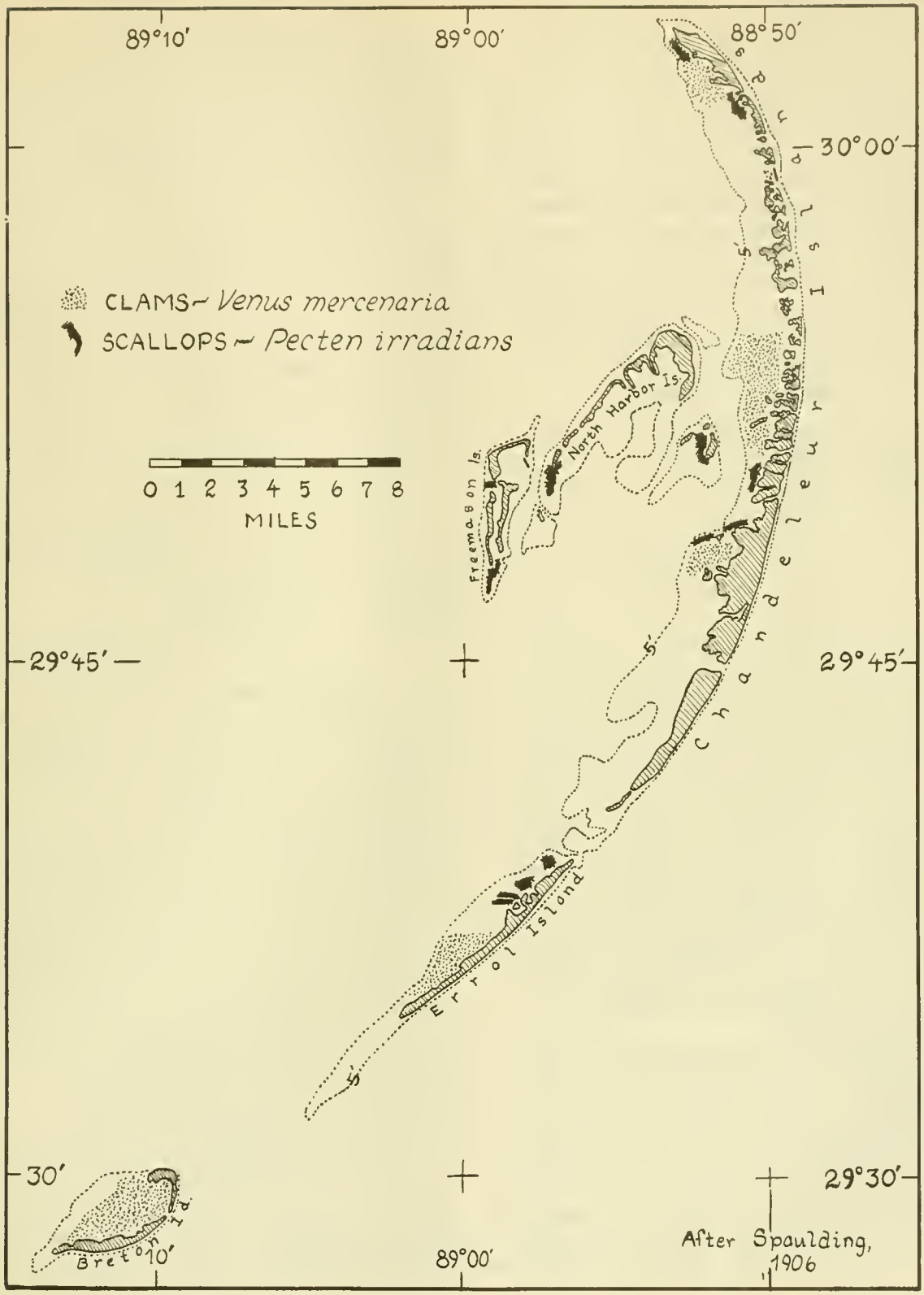

FIGURE 53.—Clam and scallop beds of the Chandeleur Islands in 1906.

preliminary results of the work east of the Mississippi delta (carried out by R. H. Parker) indicate that there is a density of 100 individual mollusks (mostly *Mulinia lateralis*) per orange peel bucket sample of 100 cu. in. capacity on some muddy bottom areas in this region. It would appear that we have here a community comparable to the *Syndosmya* (=*Abra*) community of "shallow and protected waters of an estuarine character" (Jones 1950). Such a community, composed of small, rapidly growing species, may have a rapid overturn and thus have a higher productivity in terms of harvestable crop than a community composed of larger, slower growing species. It would also be less stable.

SERPULOID REEFS

While the serpuloid reefs of Bermuda are fairly well-known to biologists, at least by hearsay, it is not generally realized that similar reefs occur in the Gulf of Mexico. There is a small area of scattered serpuloid reefs at the junction of Baffin Bay and the Laguna Madre, south of Corpus Christi, Texas, and a larger area near Veracruz, Mexico. Recent efforts to collect the worm that caused these growths in Baffin Bay have been unsuccessful, and there is some question as to whether this reef is still actively growing. According to W. Armstrong Price, there is evidence that these reefs had been actively growing within the last 80 years. The only information of the reefs near Veracruz is the brief paper by Heilprin (1890). Two reefs are mentioned; one, near Punta Gorda, was, at the time, lying parallel to shore about ⅛ mile from land, about 3/16 mile wide and about ⅝ mile in length. The other, off Punta de Hornos, was about the same size and in the same relative position to the shore line but about half as wide. A modern survey of these reefs should provide interesting information as to growth and ecology.

The serpuloid reefs of Baffin Bay are of peculiar interest in view of the high salinities which occur in this region. Salinities as high as 80 parts per thousand have been recorded, and during the period from July 1946 to October 1948 the lowest recorded salinity was 41.6 parts per thousand. Samples of serpuloid rock from this region have yielded two species of polychaetes, two amphipods and a barnacle. All the species are well-known estuarine forms.

THE JETTY COMMUNITY

There are no naturally rocky shores in the eastern or northern Gulf of Mexico, hence, there are no extensive hard-bottom communities. A limited fauna and flora has become established on the various jetties along the Texas coast and also on the short jetties at Calcasieu Pass near Cameron, but the life of the jetties on the passes of the Mississippi Delta has not been studied. The biota of the Texas jetties has been discussed by Whitten, Rosene, and Hedgpeth (1950) who describe the intertidal community of these jetties as consisting principally of three species of barnacles, a pulmonate limpet, a littorine, a species of *Brachidontes*, and various less numerous elements. Plants, an essential component of such communities, were not studied. This community was built up by colonization from nearby bottom habitats and possibly sargassum since construction of the jetties six or seven decades ago. Two motile arthropods, the isopod, *Ligia exotica*, and the almost cosmopolitan crab, *Pachygrapsus transversus*, are among the most characteristic and obvious members of this community.

Zonation is well-marked on the jetties, although the zones are narrow and vary somewhat with the season. At Port Aransas the average low-water line is marked by a belt of the brown algae, *Padina vickersae*, which extends down to extreme low water, 8 to 12 inches lower. Above the *Padina* belt is another narrow zone characteristically occupied by various red algae, especially *Gelidium*, *Bryocladia*, and the like, topped by a still narrower band of *Ulva*. In these algal zones are found such snails as *Thais* and *Cantharus*, and in the *Padina* zone are found the purple urchin, *Arbacia punctulata*, and the anemone, *Bunodosoma cavernata*. Between the top of the narrow *Ulva* belt and the maximum concentration of barnacles (*Chthamalus fragilis*) at about 2.5 to 3 feet above mean low water, there is a sparse scattering of barnacles. Above the barnacles are found the small, black littorine, *Littorina ziczac*, and the pulmonate limpet, *Siphonaria pectinata*.

There are, in summary, three principal zones on the jetty rocks and walls: an upper zone, characterized by the littorines and barnacles, a middle algal zone occupied by greens and reds, and the lower *Padina* zone. This pattern is associated with the average tidal levels for most of the year.

During the periods of lower mean sea level in January and February, the lowermost zone, below the brown algae, is exposed. This zone consists of hydroids, Bryozoa, and encrusting sponges. Inshore, near land and on concrete pilings at Port Aransas, the middle zone is also occupied by oysters. Mussels do not occur at Port Aransas but are found at Freeport and Galveston on the jetties.

Although not occurring in the Gulf of Mexico proper, the zonation in the Florida Keys and at Beaufort described by the Stephensons (1949, 1950, 1952) have aspects in common with that at Port Aransas. The most conspicuous difference is, the generally lower arrangement of the entire zonal pattern at Port Aransas in relation to tide zero, a phenomenon apparently associated with the pronounced seasonal differences in sea level on the Texas coast (fig. 54) and the higher level of the tide zero in relation to the tidal cycle.

There is a tendency toward the formation of sub-zones in Texas and Florida which may be induced by irregular tidal cycles; this complex pattern seems much less developed at Beaufort, where the tidal cycle is more regular (Hedgpeth 1953, pp. 188–194).

SAND BEACH COMMUNITIES

The communities of the sand beaches are evidently similar to those of the Beaufort area which were studied by Pearse, Humm, and Wharton (1942) since many of the same species, or closely related species, occur on the sandy beaches of Texas and Louisiana. LaFleur (1940) briefly described the biota of sand beaches of Grand Isle. Neither of these are studies of communities, in the strict sense of the term. The most noticeable bottom community of the sandy beach is that of *Donax* which occurs in large beds, moving up and down with the tides. Immediately offshore there are evidently large communities composed of such bivalves as *Dinocardium robustum*, *Arca* and *Anadara*, *Dosinia* and *Tellina*, predaceous gastropods, and such echinoderms as *Mellita* and *Astropecten*. This assemblage appears to be a counterpart of the sandy-bottom *Tellina* community of European waters.

The characteristic inhabitant of the sand beach is the ghost crab, *Ocypode albicans*, which seeks refuge during daylight hours in burrows well above high tide lines. Beyond this region, at Port Isabel and in southern Florida, there occurs the larger land crab, *Cardisoma guanhumi*. Occasional individuals are found at Port Aransas, but established colonies of them are unknown north of Port Isabel except at Grand Isle (Behre 1950). Lower down on the beach, associated with the windrows of algae (sargassum in spring and summer and various reds in winter) are the amphipods, *Orchestia grillus*, *O. platensis*, and *Talorchestia longicornis*.

Intensive study of the animal life of this most characteristic of Gulf coast environments has hardly begun. Caspers (1951), in a study of the arthropods of the Bulgarian coast, characterized the community of the sandy beaches as the "*Orchestia* variation of the *Pachygrapsus* biocoenosis." From the vantage point of the Texas coast where *Pachygrapsus* seems most abundant on the jetties and the sand constitutes the major part of the environment, we might say that *Pachygrapsus* is a "variation" of the "*Orchestia* (or *Ocypode*) biocoenosis."

THE SHRIMP GROUND COMMUNITY

Offshore in the muddy bottoms between the foot of the sandy beach and the 10- to 15-fathom line there occurs a large community which we recognize principally as that from which white shrimp, *Penaeus setiferus*, are taken in commercial quantities. Several sedentary invertebrates are characteristic of these bottoms. The most conspicuous of these is the sea pansy, *Renilla mülleri*, which must pave the bottom in some localities. A gorgonian, *Leptogorgia setacea*, also flourishes in this region. Other characteristic members of this shrimp ground community include tube building worms of the family Onuphidae, crabs of the genera *Hepatus*, *Calappa*, and *Persephone*, the anemone, *Paranthus rapiformis*, and certain gastropods, e. g., *Busycon*, *Murex*, *Dolium*, and *Fasciolaria*. In the larger abandoned shells of these snails there occurs the large red hermit crab, *Petrochirus bahamensis*. Usually the shells bear one or more anemones, *Calliactis tricolor*, and inside, living commensally with the hermit crab, is the porcelain crab, *Porcellana sayana*. Also common, but perhaps occurring in irregular colonies, is the stomatopod, *Squilla empusa*.

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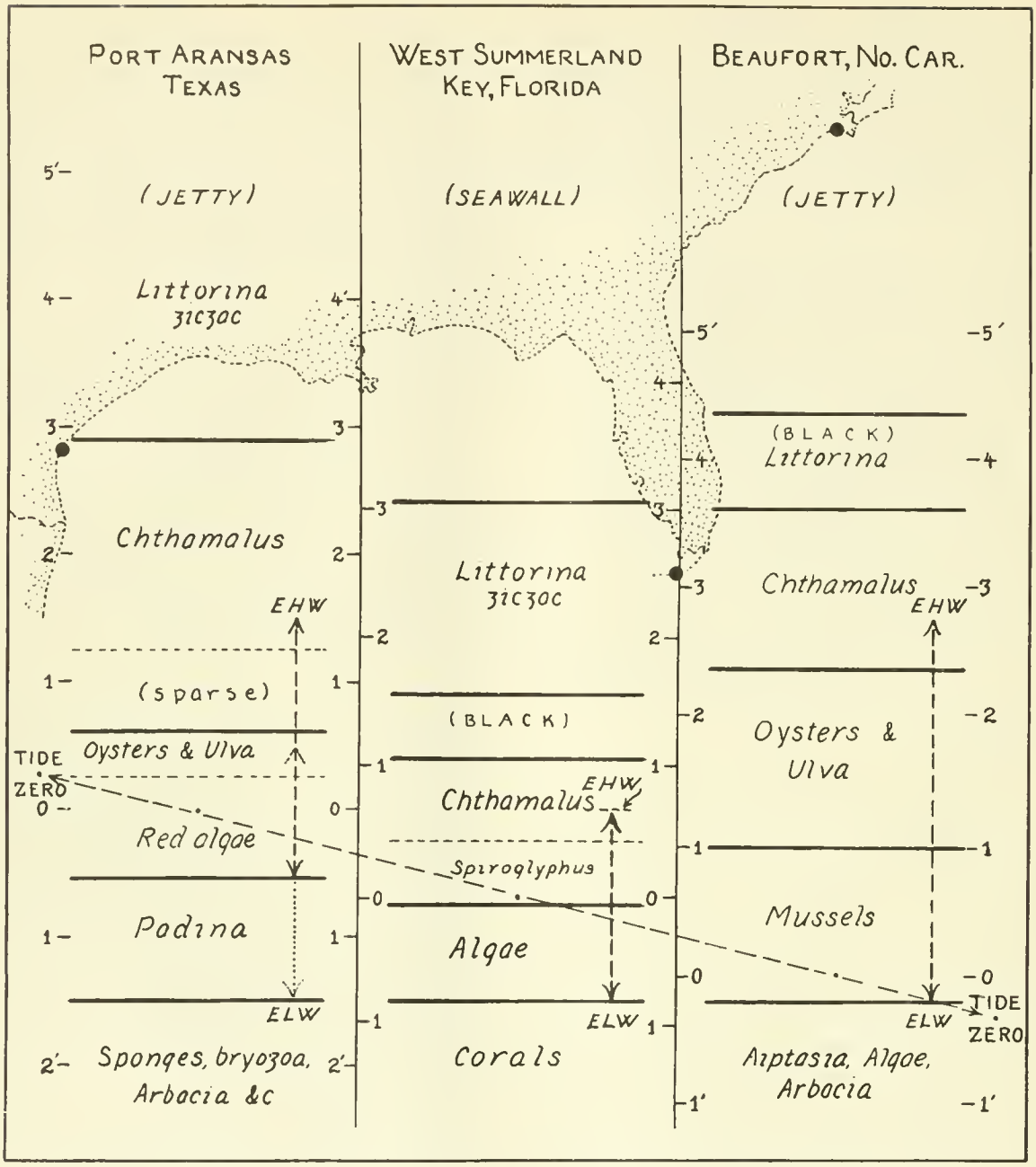

FIGURE 54.—Pattern of distribution of organisms on jetties and sea wall in Port Aransas, Texas, West Summerland Key, Florida, and Beaufort, North Carolina.

The preceding description applies principally to the grounds frequented by the commercial shrimp, *Penaeus setiferus*. The recent change in the shrimp fishery toward exploitation of the populations of the brown or grooved shrimp, *P. aztecus*, has revealed some differences in the constitution of the bottom communities frequented by *P. aztecus*. *Renilla* is no longer characteristic, but one of the *Astropectens* is abundant, and two bivalves, *Pitaria cordata* and *Chione clenchi*, are much more abundant than they are closer inshore on the *P. setiferus* grounds. The principal region occupied by the pink shrimp, *P. duorarum*, is near Key West across the Strait from Campeche Bank

(fig. 51), the fauna of which is predominantly tropical in character.

The communities which support penaeid shrimp appear to have no counterpart in European waters, but similar communities evidently occur in waters of southeastern Asia and along the western coast of Central America. It is worthy of note that the commercial fishery of shrimp is one of the few major fisheries drawing upon an annual (or perhaps biennial) production and is thus more dependent on the short term production of bottom fauna and short-term secular changes in the environment than are the fisheries which exploit organisms that have required several years to reach marketable size.

THE CORAL AND SPONGE COMMUNITIES

These are tropical, stenohaline communities, rich in number of species and difficult to characterize except in terms of their dominant members. The reef-building coral is a true community dominant, shaping the community and altering the environment. The small reefs or patches along the Texas and Louisiana coast are peculiar northern fragments of the West Indian reefs. Their position is governed primarily by the occurrence of small elevations along the edge of the continental shelf which rise to within 10 to 25 fathoms of the surface rather than by temperature or sedimentation conditions. These elevations may indicate dome structures. It can be inferred from the presence of these living reefs that the mean temperatures do not fall below 20° C. along the summits of these structures. There are rare records of tropical reef animals, especially decapod Crustacea, along the Texas coast indicating that these reefs have the usual West Indian tropical fauna and that a certain amount of straying, especially during the summer months, occurs. More information concerning the sponge and coral communities of western Florida will be found in other parts of this volume.

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CHAPTER VI

BACTERIA, FUNGI, AND UNICELLULAR ALGAE

MARINE BACTERIA AND FUNGI IN THE GULF OF MEXICO[1]

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Although the marine environment around the West Indies was one of the first to be examined by a bacteriologist (Fischer 1886) and has since been quite extensively studied (Drew 1912; Bavendamm 1932), there are very few published reports on bacteria and fungi in the nearby Gulf of Mexico. The author has been actively interested in the Gulf coast area since 1940, but the semiconfidential nature of the research projects has contraindicated the publication of the results. This paper summarizes personal observations in the region along with published reports that have a direct bearing upon microbiological conditions in the Gulf of Mexico where observations have been confined almost exclusively to regions near shore. The rather extensive but scattered literature on marine microbiology has been reviewed by Issatchenko (1914), Bavendamm (1932), Benecke (1933), ZoBell and Upham (1944), and ZoBell (1946a, 1947). Also noteworthy is the comprehensive article by Williams (1951) on the occurrence, importance, and characteristics of bacteria in the sea.

Waters of the littoral zone in the Gulf of Mexico are veritable bacterial gardens. At scattered stations from Tortugas to Aransas Pass, where water samples have been examined, bacterial populations ranging from thousands to many million per ml. have been observed. Large numbers of living bacteria have also been found in bottom sediments. The methods employed by various investigators for collecting and analyzing samples of water and marine sediments for numbers and kinds of bacteria have been summarized by ZoBell (1946a).

The abundance of bacteria in shallow Gulf waters, which greatly exceeds the abundance of bacteria in the open ocean, is believed to be attributable primarily to the higher content in the former of organic matter and suspended solids, both of which promote the growth of bacteria. The influx of fresh water with its load of organic nutrients from land drainage is also a contributing factor along the littoral zone. Here there is a commingling of both fresh-water and marine microorganisms and numerous transitional stages of both kinds. The observations of Berkeley (1919), Korinek (1926), Lipman (1926), Burke and Baird (1931), ZoBell and Feltham (1933), Burke (1934), and others indicate that ordinarily bacteria from fresh-water or terrestrial sources do not survive very long in sea water, but if the transition to the salt-water environment is gradual, as in brackish water of increasing salinity, a good many fresh-water forms may become acclimated to the marine environment (ZoBell and Michener 1938).

The bacterial flora of the Gulf coast region is characterized by exceptional biochemical versatility, cultures having been isolated that catalyze the transformation of virtually all types of organic matter and a good many inorganic substances. In the latter category are autotrophic bacteria of various kinds that oxidize hydrogen sulfide either in darkness or under the influence of sunlight (van Niel 1931, 1944). Autotrophs which oxidize ammonia to nitrite appear to be more common in surface water and sediment than those which oxidize nitrite to nitrate (Carey 1938). Methane oxidizers (Hutton and ZoBell 1949) were found in the topmost portions of mud samples from the Gulf coast region, and sulfate-reducing bacteria which oxidize molecular hydrogen as the sole source of energy were found in numerous samples from considerable depth (Sisler and ZoBell 1950).

Besides modifying inorganic substances, autotrophic bacteria are primary producers of organic matter. While some obtain their energy from sunlight in the manner of other photosynthetic plants, most autotrophic bacteria obtain their energy for the reduction of carbon dioxide from the oxidation of substances such as hydrogen sulfide, hydrogen, methane, ammonia, or nitrite.

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Quantitative data on the relative amounts of organic matter synthesized by autotrophic bacteria are not available, but judging from the abundance of such bacteria and the quantities of ammonia, hydrogen, methane, or other substance believed to be oxidized, organic production from this source may be appreciable.

The chief function, however, of bacteria in the marine environment is in the mineralization or modification of organic matter (Waksman 1934). Among the organic materials found to be attacked by marine micro-organisms are sugars, starches, celluloses (Bavendamm 1932; Waksman et al., 1933), pectins, glucosides, fatty acids (Thayer 1931), triglycerides, alcohols, sterols, proteins, amino acids, chitins (Hock 1940), lignins, agar (Stanier 1941; Humm 1946), and hydrocarbons (ZoBell 1950a). These organic substances are attacked by both aerobic and anaerobic bacteria.

From Gulf of Mexico mud, Campbell and Williams (1951) isolated 20 strains of aerobic chitin-decomposing bacteria, including species of *Achromobacter*, *Flavobacterium*, *Micrococcus*, and *Pseudomonas*. Several of the cultures were actively proteolytic and/or lipolytic.

Mixed cultures from marine mud tend to decompose the organic remains of plants and animals (Waksman 1934) in aerobic environments with the formation of carbon dioxide, ammonia, sulfate, phosphate, and other oxidation products at a rate which is primarily a function of the temperature. In the absence of free oxygen the rate at which organic matter is modified by bacteria may be much slower, and, while there may be much mineralization of organic substances, in anaerobic environments certain constituents may be reduced or hydrogenated to form the mother substance of petroleum (ZoBell 1950b).

The action of heterotrophic bacteria is not confined to the decomposition of particulate organic materials. Dissolved organic matter is also utilized, it having been shown by ZoBell and Grant (1943) that under static conditions bacteria may reduce the organic content of sea water to less than 0.1 mgm./L. According to Waksman and Carey (1935), roughly 60 percent of the organic carbon is oxidized by aerobes to carbon dioxide and the remaining 40 percent is assimilated for conversion into bacterial protoplasm. The latter, being particulate, becomes available as a source of food for protozoa, copepods, filter feeders, detritus feeders, and grazing animals in general.

Krizencky and Podhradsky (1927) regard the conversion of dissolved organic matter into particulate matter utilizable by animals as one of the most important functions of bacteria in aquatic environments. The importance of bacteria as food for animals has been emphasized by the work of Baier (1935), MacGinitie (1935), Voroschilova and Dianova (1937), Mare (1942), and ZoBell and Feltham (1938). The latter workers (1942) estimated that around 10 grams (dry weight) of bacterial organic matter is produced per day per cubic foot of mud in a shallow marine mud flat. In summarizing the ecological function of bacteria on sand beaches, Pearse et al. (1942) point out that besides serving as food for small animals, bacteria are important scavengers, and they produce plant nutrients, including ammonia, nitrite, nitrate, and phosphate. From thousands to millions of living bacteria were found in beach sands at Beaufort, North Carolina.

Large numbers of bacteria were found by Williams et al. (1952), to be associated with the bay shrimp, *Penaeus setiferus*, taken from Aransas Bay and from the Gulf in the region of Galveston. Species of *Achromobacter*, *Bacillus*, *Micrococcus*, *Pseudomonas*, *Alcaligenes*, and *Flavobacterium* predominated in the order named. Most of the attached bacteria were carried by the cephlothorax portion of the shrimp. The optimum temperature for the growth of the bacteria was around 25° C., but most of the 1,200 cultures examined grew slowly at 4° C. Neither coliforms nor enterococci were detected by Williams and Rees (1952) in the intestinal tract of shrimp, suggesting that such bacteria have sanitary significance.

Another important function of bacteria is as symbionts in the alimentary canal of most marine animals where they aid in the digestion of chitin, cellulose, pectin, lignin, and other organic complexes. Similarly, certain shipworms and wood borers are believed to depend upon commensal bacteria which help to digest cellulose and lignin.

On the other hand, a small percentage of the microbial flora is pathogenic for plants or animals. Fish, Crustacea, shellfish, and other marine animals in nearly all stages of development may be susceptible to microbial infections; the pertinent

literature on this subject has been annotated by ZoBell (1946a). Seaweeds, diatoms, dinoflagellates, and other marine plants may be extensively parasitized by pathogenic bacteria, actinomyces, yeasts, and mold fungi. The wasting disease of eelgrass, which threatened the extermination of *Zostera marina* along the Atlantic seacoast a few years ago, is believed to be due to infection by *Labyrinthula* species (Renn 1936), although *Halophiobolus* species may also be involved (Barghoorn and Linder, 1944).

By vitiating the water in local environments or in the wake of periods of intense organic productivity, bacteria may have far-reaching adverse effects on the plant and animal populations. Among the ways in which bacteria contribute to the vitiation of aquatic environments are by depleting dissolved oxygen, by producing hydrogen sulfide, by forming toxic amines, or by changing the pH of the water. So-called stagnant water basins are rendered uninhabitable primarily by the activities of bacteria, and extensive areas in the open ocean may become temporarily lethal for plants or animals. For example, Copenhagen (1934) described an area approximately 25 by 200 miles in the Atlantic Ocean off Walvis Bay, South Africa, where hydrogen sulfide is liberated periodically by bacterial activity in quantities sufficient to kill both flora and fauna. The bacterial vitiation of water is believed by the writer to be an important feature of the "red tide." Extensive populations of purple sulfur bacteria, observed by Gietzen (1931) growing associated with decomposing algae along the Holstein coast, imparted a distinctly red coloration to the sea.

Marine bacteria also contribute to the biofouling of man-made structures. The attachment and growth of barnacles, bryozoans, tunicates, mussels, clams, algae, and other fouling organisms on ships' bottoms or other submerged surfaces may be promoted by bacteria in various ways (ZoBell and Allen 1935). Likewise, micro-organisms may contribute either directly or indirectly to the deterioration of pilings, planks, and other wooden structures in sea water. Lines, ropes, nets, seines, sailcloth, and other cordage or textile products readily rot in sea water unless they are treated to preserve them from microbial decomposition (Atkins and Warren 1941). Unprotected steel and iron structures are also susceptible to attack by bacteria which oxidize ferrous iron, produce acids, form hydrogen sulfide, create reducing conditions, or depolarize hydrogen films resulting from the reaction between water and iron. Acid production in microspheres from the bacterial oxidation of organic matter or sulfur may result in the corrosion of concrete. Even rubber and bituminous coating materials may be attacked by marine micro-organisms (ZoBell 1950a).

Bacteria are important chemical and geological agents in marine bottom deposits where they promote many processes involving organic compounds, inorganic constituents, and physicochemical conditions that affect the modification or diagenesis of sediments. One of the first geochemical processes to be studied by microbiologists was calcium carbonate precipitation which Drew (1911a, b) attributed to the activities of denitrifying bacteria found in great abundance in shallow subtropical seas in the vicinity of Jamaica and Tortugas. He (1912) reported that marine mud near the Bahamas contained an average of 160 million bacteria per ml. with *Bacillus calcis* predominating. Working in the same region, Kellerman and Smith (1914) confirmed Drew's hypothesis on the precipitation of calcium carbonate by bacteria which raise the pH by reducing nitrate, by producing ammonia, or by utilizing organic acids.

After finding rather sparse bacterial populations in the open sea around Tortugas, Lipman (1929) questioned whether bacteria contribute significantly to calcium carbonate precipitation. This view was rendered untenable, however, by the extensive observations in the Bahamas of Bavendamm (1932) who concluded that calcium carbonate precipitation in tropical seas is primarily a microbiological process. Similar conclusions were reached by Gee (1932) who investigated bacterial activity in the Florida Keys. Micro-organisms found there by Gee and Feltham (1932) promoted the precipitation of calcium carbonate by producing ammonia and otherwise increasing the pH.

The pH of marine sediments may be increased by micro-organisms which (1) form ammonia, (2) reduce nitrate or nitrite, (3) reduce sulfate, (4) oxidize or decarboxylate organic acids, or (5) utilize CO_2. On the other hand, the (1) production of CO_2 or organic acids, (2) oxidation of

hydrogen sulfide or sulfur, (3) formation of nitrate, (4) assimilation of ammonia, or (5) the liberation of phosphate from organic compounds are microbial processes that tend to decrease the pH of their environment. Reactions ranging from pH 6.8 to 8.7 in Gulf coast sediments are believed to be attributable, at least in part, to microbial activities. Similarly, bacteria and allied microorganisms are believed to be the principal dynamic agencies that create conditions in marine sediments sometimes as reducing as E_h—460 millivolts (ZoBell 1946b).

The general tendency is for micro-organisms to mineralize the organic remains of plants and animals in marine sediments. In highly reducing environments, however, the microbial decomposition of organic matter may result in residues relatively richer in hydrogen and correspondingly poorer in oxygen, nitrogen, sulfur, and phosphorus. This results in the accumulation of organic complexes that are more petroleum-like than their predecessors (ZoBell 1950b). The microbial formation of methane is a common property of recent marine sediments, and there is pretty good evidence that bacteria also produce higher hydrocarbons. While there is no reason to believe that bacteria produce petroleum, they may contribute in many ways to its formation. The high organic productivity and rapid rate of sedimentation in Gulf coast waters suggest this region as a potential source bed of petroleum.

Petroleum hydrocarbons may be modified in recent sediments by micro-organisms. Both aerobic and anaerobic bacteria which attack petroleum hydrocarbons were detected in nearly all 1-gram samples of surface mud collected from shallow water along the coasts of Louisiana and Texas. From hundreds to millions of such micro-organisms per gram of mud were demonstrated by the minimum dilution method.

Sulfate-reducing bacteria were also found in abundance, some at core depths exceeding a hundred feet. Sulfate reducers form hydrogen sulfide, and they may account for the formation of sulfur. The recovery of sulfate reducers having unique tolerance for temperature, salinity, and hydrostatic pressure from oil and sulfur wells suggests that they may be indigenous species in ancient marine sediments (ZoBell and Rittenberg 1948). A large percentage of the sulfate reducers isolated from Gulf coast sediments can utilize molecular hydrogen (Sisler and ZoBell 1950).

Several other physiological types of bacteria, that may function as geochemical agents, have been found in marine sediments, but their importance can be assessed only after they have been more thoroughly studied.

Marine fungi, including yeasts and molds, are found almost exclusively in water and the topmost layers of sediment. Being heterotrophs, such fungi are closely associated with organic substances. Both yeasts and molds commonly occur growing either saprophytically or parasitically on marine plants and animals. According to Sparrow (1936), who isolated 18 new species of mold fungi from the Woods Hole region, marine fungi have been even less completely studied than marine bacteria. Barghoorn and Linder (1944) were impressed by the diversity of fungi found in the sea. A good many of the fungi species isolated from the sea are quite unlike any known terrestrial species. They grew better in sea water than in corresponding fresh water media, and some species developed in media containing three times as much salt as normal sea water.

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DINOFLAGELLATES OF THE GULF OF MEXICO

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Dinoflagellates are important in the natural economy of the Gulf of Mexico as they are in all waters of the world. In marine phytoplankton they are usually outnumbered by diatoms, but they are second in importance to the diatoms as fundamental synthesizers of organic material in the sea. On the other hand, to the dinoflagellates belong most of the organisms which cause "red water," mass mortality of marine organisms, and paralytic shellfish poisoning. A thorough knowledge of the dinoflagellates is necessary to a clear understanding of the basic biology of the Gulf of Mexico.

Despite the importance of these organisms, the Gulf of Mexico is almost a terra incognita in respect to our knowledge of the dinoflagellate plankton. Very few oceanographic expeditions have included the Gulf in their itinerary, and those that visited the Gulf have not reported on any dinoflagellate collections.

Many species of dinoflagellates have a world-wide distribution, especially the offshore forms. Many of these can be expected in the Gulf. It is very likely that the pelagic species of the Gulf will be found to be similar to those of the tropical Atlantic, although the general composition of the flora may be different. The inshore, or neritic, plankton may well contain species peculiar to or at least characteristic of the Gulf of Mexico or of certain areas of the coast line. The dinoflagellate fauna of the open Gulf is very likely quite similar to that of the Caribbean and the tropical Atlantic.

As far as the dinoflagellates are concerned, there are three general habitats in the Gulf of Mexico: the offshore waters, the neritic waters, and the sandy beaches.

The offshore waters of the Gulf are clear and blue, characteristic of tropical waters the world over. Surface temperatures are high, the concentration of nutrients is low, and the salinity high throughout the year. The quantity of plankton in these waters (the standing crop) is low (Riley 1938), but the number of species is probably relatively high. The temperature of this water drops markedly in the northern part of the Gulf for a few weeks during the winter, but as far as we know there is no seasonal change in the dinoflagellate fauna during this period.

The neritic waters may be considered to include the shallow periphery of the open Gulf in which the water is often of very high temperature, with variable salinity and nutrient content and in which wind mixing creates high turbidity, particularly in the winter when the density of the water is uniform from surface to bottom. The bays, bayous, and lagoons are also within this zone. These include mangrove swamps and other brackish water areas. Tidal effects are strong in the neritic zone, and the physical and chemical conditions of the water vary greatly throughout the year and, in some cases, within a daily tidal cycle. As a general rule, the species of dinoflagellates found in the neritic zone are distinct from those in open waters. However, the invasion of the coastal area with open Gulf water frequently obscures the zonation.

Sandy beaches in the intertidal zone constitute the third type of environment for the Gulf dinoflagellates. Certain specialized species belonging chiefly to the genus *Amphidinium* thrive in this situation in some parts of the world (Herdman 1924) causing discoloration of the sand and luminescence. When they are abundant, each kick of the heel at night on a wet, sandy beach will cause a flash of light. There are apparently no reports of such "dinoflagellate sand" for the Gulf coast, but a careful investigation of this zone might reveal a rich fauna.

Interest in the dinoflagellates of the Gulf, particularly along the west coast of Florida, was stimulated by the disastrous outbreaks of red tide which occurred in that area in 1946 and 1947 (Galtsoff, 1948; Gunter et al., 1948; Gunter, Smith, and Williams, 1947; Smith 1949). This red water was caused by a previously undescribed species, *Gymnodinium brevis* Davis (1948). The

study of the causes of these outbreaks was hampered by the lack of previous work in the area. As a consequence, the Marine Laboratory of the University of Miami and the Fish and Wildlife Service of the United States Department of the Interior initiated a study of the local plankton in order to gain some information regarding the causes of such plankton blooms. In the course of these studies some insight was gained of the normal dinoflagellate plankton along the west coast of Florida.

Davis (1950) reported upon a number of plankton samples collected there in 1947 and 1948. He listed 15 species of dinoflagellates.

He stated that the plankton of the west coast of Florida is markedly different from that of the east coast of Florida. Species found only on the west coast included the dinoflagellates, *G. brevis* and *Noctiluca scintillans* Macartney, which were found both inshore and offshore. In addition, a number of plankters were found only in the open waters of the Gulf. These included *Ceratocorys horrida* Stein.

Some species were found only in open waters but on both coasts. This group consisted of *Ceratium candelabrum* (Ehr.) Stein, *Pyrocystis fusiformis* W. Thomson, and *P. noctiluca* Murray. Occasionally, the open water species were found inshore. Davis interpreted this as indicating an admixture of open water with the inshore water. Davis and Williams (1950) listed seven species from brackish water in mangrove areas of southern Florida.

King (1950) listed 19 species of dinoflagellates from the west coast of Florida in a series of samples extending from inshore bays to a distance of 120 miles offshore and collected over a period of 10 months in 1949. About 10 of these species were not listed by Davis or Davis and Williams.

Additional species have been found by John Howell, biologist, Fish and Wildlife Service (unpublished data), along the west coast of Florida. *Ceratium pentagonum* Gourret occurred only at stations more than 30 miles offshore. A species of *Pyrocystis* (*Gymnodinium*) was present only offshore except in one sample. In a study of samples collected throughout the year Howell found the most commonly occurring species of dinoflagellates to be *Ceratium furca* (Ehr.) Dujardin and *C. tripos* (O. F. Muller) Nitzsch. Next in order of occurrence were *C. macroceros* (Ehr.) Vanhoffen, *C. fusus* (Ehr.) Dujardin, *C. trichoceros* (Ehr.) Kofoid, *C. massilliense* (Gour.) Jörgensen *Peridinium depressum* Bailey, and *Dinophysis caudata* Saville-Kent. All of these appear to occur inshore as well as in the offshore waters of the Gulf. However, a more intensive study of the distribution of dinoflagellates along the coast may bring out more zonation than is at present apparent. The situation is complicated by the fact that typical open Gulf water with high salinity, low nutrient content, etc., sometimes extends up to the beach and, indeed, is carried into the bays by tidal action.

Howell found 11 species not reported by Davis or King. In addition to those listed above, there were 4 species of *Ceratium: C. carriense* Gourret, *C. horridum* Gran., *C. falcatum* (Kof.) Jörgensen, *C. praelongum* (Lem.) Kofoid. The last-named was found only once and is typical of a large number of very rare species which may be expected to be found occasionally in the open Gulf waters if any extensive investigation of these waters is made.

Other rare species found by Howell were *Pyrocystis hamulus* Cleve, *Pyrophacus horologicum* Stein, *Amphisolenia* sp., *Goniodoma* sp., and *Ornithocercus quadratus* Schütt. In a laboratory culture of Florida west coast water *Oxyrrhis marina* Dujardin flourished, and a large population developed.

Despite the richness of the dinoflagellate fauna in the Gulf, the actual concentration in terms of populations is normally very low. The concentration of dinoflagellates in numbers of cells per liter of sea water is usually less than 50 in the waters along the west coast of Florida. Yet, under unusual conditions which are still not clearly understood, a particular species may increase to enormous concentrations and cause serious disruption of the normal biological balance in the area involved.

Thus, in the Florida red tide of 1946 and 1947 the concentrations of *Gymnodinium brevis* Davis reached 60 million cells per liter (Davis 1948). These enormous concentrations cause the water to turn color, usually a brownish red, producing what is commonly called "red water" or "red tide." [1] Such concentrations of dinoflaggellates are frequently accompanied by the death of fish

[1] Red tide in the Gulf of Mexico waters is discussed in an article by R. Lasker and F. G. Walton Smith pp. 173–176.

and other marine animals. There is every reason to believe that many species of dinoflagellates elaborate an extremely potent toxin either normally or under the conditions of population crowding. The two blooms cited above were associated with serious "fish kills" and death of much of the marine life in the area.

The presence of even normal numbers of dinoflagellates in the water may cause shellfish to become unfit for human consumption. Thus, regularly during the summer months the California sea mussel (*Mytilus californianus*) is likely to be lethal to humans when *Gonyaulax catenella* Whedon & Kofoid is abundant in the coastal water (Sommer et al., 1937), and the clams in certain areas of the Bay of Fundy are regularly toxic when *Gonyaulax tamarensis* Lebour occurs in the plankton (Medcof et al., 1947). Paralytic shellfish poisoning caused by eating such toxic shellfish has not been reported from the Gulf of Mexico. Connell and Cross (1950) found a dinoflagellate resembling *Gonyaulax catenella* associated with the death of fish in Offatts Bayou, an inlet of Galveston Bay, in 1949. Unfortunately, no specific identification of this organism was made. There is also strong evidence that the fish kills which regularly occur in Offatts Bayou are generally caused by the production of hydrogen sulfide or to suffocation due to stagnant conditions at the inner end of the inlet (Gunter 1942, 1951) rather than by a dinoflagellate bloom.

Toxic red water such as occurs regularly in the pearl oyster beds in Japan (Mitsukuri 1904) could be disastrous to the vast oyster industry in the Gulf, but apparently the Gulf oysters have been spared any such visitation so far.

Reports of red water on Campeche Banks, off Yucatán, are made occasionally by fishermen in that area, but to date it has not been possible to ascertain the causative agent. It is quite possible that a dinoflagellate is involved.

One of the great difficulties in dinoflagellate research is the fragility of the naked forms. Many of these are almost impossible to preserve but must be studied alive under the microscope. This feature might not be serious if the organisms were easily cultured, but they are notoriously difficult to grow in the laboratory. The classical monograph of the unarmored dinoflagellates by Kofoid and Swezy (1921) was based largely on examination of living specimens which regularly dissolved before the eyes of the workers as they studied them. The Florida red tide was caused by such a naked form, *G. brevis*, which does not preserve in formalin. Special fixatives such as Bouin's solution and Schaudinn's solution do preserve some of these species but not without distortion.

However, a rich fauna of unarmored forms is not normally present inshore at Sarasota, Florida, where the workers of the Fish and Wildlife Service laboratory in their search for *G. brevis* have examined living material for 2 years and failed to reveal any *G. brevis*. They found only three other species of unarmored dinoflagellates. More work in other areas must be conducted before this problem can be solved.

The difficulty in making specific identification of dinoflagellates has lead to a paucity of records of these interesting and important organisms. Painstaking microscopic work on the part of a specialist is necessary for the differentiation of many species, even of the thecate forms which preserve well.

In these species, an analysis of the plate pattern is necessary for identification. Few general planktologists have either the time or training to pursue this kind of work which involves difficult micro-orientation and dissection. Concentrated study by a number of specialists for a considerable period of time will be necessary before the dinoflagellate plankton of the Gulf will be adequately revealed to science.

Since most of the pelagic tropical species of dinoflagellates are worldwide in distribution, published works for other areas can be used for a study of the Gulf fauna. The most important of these are listed in the bibliography. Lebour's (1925) work is designed for northern seas but includes many tropical species. It is a very useful treatise, especially for a beginner who needs orientation. Kofoid and Swezy's (1921) monograph is a classic on the naked forms but must be augmented by later papers. Kofoid and Skogsberg's (1928) Dinophysoidae is another classic and covers that group in a comprehensive manner. The Heterodiniidae has been monographed by Kofoid and Adamson (1933). Most of the Peridiniidae are in need of monographic treatment. It is very difficult to identify the smaller species with present literature. For the Ceratia Jorgensen's (1911) monograph and Graham and

Bronikovsky's (1944) treatise on *Carnegie* Ceratia are quite useful. The most comprehensive systematic treatment of the dinoflagellates as a group is Schiller's Dinoflagellata in Rabenhorst's Cryptogamen-Flora (1931–37). The reports of the larger world expeditions complete the general literature on dinoflagellate taxonomy. Such references are included in the bibliography.

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PRESENT STATUS OF DIATOM STUDIES IN THE GULF OF MEXICO[1]

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Very little concerted work has been done on the diatoms of the Gulf of Mexico region to date. Considering its size and diversity of habitat, the Gulf is a virtually untouched area in this regard. The few studies made have been of a somewhat casual, quite limited, and localized nature leaving almost the entire shoreline and open water area of the Gulf completely unexplored.

Previous records are confined mainly to the southwest corner of the Gulf (Campeche Bay), Mobile Bay on the north, the west coast of Florida (Tampa and Pensacola Bays), the Dry Tortugas, and a few in the West Indies, with fragmentary, unpublished records from a few other places. Few, or almost none of these (see bibliography), are well-defined floristic studies. A number of works on diatoms of Honduras and Caribbean waters, not within the Gulf region but closely allied to it in character of flora, add useful supplementary records.

Most of the previous efforts have been concerned with mere identification of species with very little data as to precise location, date of occurrence, and habitat. Many of the early listings are included in Schmidt's Atlas der Diatomaceenkunde (1876) with references only to the locality but without any further information. Despite the dearth of published records and the very limited territory explored the writer was able to compile from several sources a list (unpublished) comprising some 60 genera and about 500 species and varieties. The list is incomplete, however, and gives no assurance of what diatoms one may expect to find in the Gulf, because virtually no work has been done so far on the pelagic species, their succession and seasonal fluctuations. The diatom flora of many shallow water indentations of the shoreline, of swamps and reefs will also require further studies.

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LITERATURE

In the appended bibliography are given only those papers which apply specifically to the Gulf or Caribbean waters and such few general works which include the forms found there. For reliable description of the species concerned it is necessary to consult such useful works as A. Schmidt's Atlas der Diatomaceenkunde (1876), H. Van Heurck's Synopsis des Diatomées de Belgique (1880–85); and H. and M. Peragallo's Diatomées Marines de France (1897–1908). Many of the papers dealing specifically with Gulf diatoms are merely lists of species or brief unillustrated accounts which cannot be used for identification.

The distribution of many diatoms is so widespread that it is sometimes necessary, and quite satisfactory, to rely for their identification on literature pertaining to areas entirely remote from the one in question. This is true not only of the free-floating species, but also of many bottom-dwelling and attached forms, such as, for instance, *Melosira sulcata* and *Actinoptychus undulatus*, which, despite a sedentary existence, are widely dispersed.

The standard plankton works of Gran, Nordisches Plankton (1905), and Marie Lebour's Plankton Diatoms of Northern Seas (1930), will be found applicable to a goodly number of tropical forms, especially the *Rhizosolenias* and *Chaetoceros* species, and other typical plankton diatoms although there may be some species in the Gulf waters which will not be found in these publications.

CAMPECHE BAY

Mann (1925) called attention to the remarkable correspondence between the diatom flora of the Campeche Bay in the Gulf of Mexico to that of the waters around the Philippine Islands. The list included by him in the introduction to his paper contains 78 forms common to both places

including 28 not found elsewhere. Both floras are characterized also by a number of remarkable species of *Campylodiscus*. As an explanation, Mann implies the possibility of parallel development and discounts the idea of transfer or dispersal between the two localities. Other workers take exceptions to the whole idea of attaching any significance to the common appearance of diatom species in the two widely separated areas. At least, it is an interesting observation and one not to be neglected.

Among the Campeche Bay diatoms, mostly registered in Schmidt's Atlas (1876–) are many species and varieties bearing the name *campechiana*, such as *Amphora crassa* Greg. var. *campechiana* Grun., *A. grevilleana* Greg. var. *campechiana* Grun., *Campylodiscus campechianus* Deby, *Cocconeis campechiana* Cleve, *Cosinodiscus gemifer* Ehr. var. *campechianus* Ratt., *C. marginulatus* Ratt. var. *campechiana* Grun., *Endictya campechiana* Grun., *Glyphodesmis campechiana* Boyer, *Navicula campechiana* Grun., *Nitzchia campechiana* Grun., *Stephanopyxis campechiana* Grun., *Surirella campechiana* Hust., *Triceratium campechianum* (Grun.?), and others, indicating a very diverse and novel flora. Yet we have little information as to the exact source and extent of the material from this sizeable area, and it is likely that more thorough and careful survey may add new findings to this apparently most interesting locality.

If the great diversity of the Campeche Bay diatom flora and the yield of new forms is any indication of what might be expected from examination of other places in the long stretches of unexplored shore line of the Gulf, interesting prospects are in order. It must be remembered, however, that the yield of new forms from Campeche Bay came mostly many years ago when fewer species were known from other places.

MOBILE BAY

Probably one of the more intensively studied areas of the Gulf coast thus far is Mobile Bay. A list of diatoms from this area published by Cunningham (1889), one of the few diatom students local to the Gulf area, includes 37 genera and 137 species, but is probably far from complete. Cox (1901) who identified the diatoms in Cunningham's collection, furnished a useful but clearly incomplete list of 29 genera and 62 species. This material obtained from George H. Taylor, Wm. McNeil, and his own collecting, includes typically fresh water, brackish, and marine forms. Since Cox specifically says that all the specimens are from Mobile Bay it is obvious that fresh water species in this collection were brought in by streams. This list is also correlated with records of George H. Taylor from Tampa Bay.

One form from salt marshes at Mobile found in Cunningham's material and named by Grunow is sufficiently remarkable and well known to deserve particular mention. It is *Terpsinöe intermedia* Grun., a diatom of abnormal structure with quite symmetrical adjutment on the central, valve face (see Schmidt's Atlas, 1876, plates 198–200). The species is closely related to *T. musica* Ehr., typical of the Gulf coast. It is evidently plentiful in its original locality near Mobile.

TORTUGAS AND WEST COAST OF FLORIDA

Extensive collections made by the writer at Tortugas and around Tampa Bay are in process of study, and some observations based on them are included in this summary. George H. Taylor made records from Tampa Bay as above cited. Mann prepared a list of diatoms of Pensacola Bay. The writer's report (unpublished) on plankton diatoms of the west Florida coast, off Tampa and Fort Myers, to E. Lowe Pierce of the University of Florida, includes 35 genera and 82 species and varieties. Some species of *Chaetoceros* and *Hemidiscus* included in this list were found in heavy concentrations, a fact which indicates that Gulf coastal waters are, at times, very productive.

From the studies mentioned above an inference may be drawn that mixed calcareous and organic muds of the west coast of Florida provide favorable environment and adequate supply of nutrients to support a generally rich and varied diatom flora which includes, conspicuously, forms like *Terpsinöe musica*, *Biddulphia rhombus*, *Isthmia capensis*, *Auliscus*, *Aulacodiscus*, *Navicula*, and others.

OTHER RECORDS

Diatom records made in connection with oil-pollution investigations conducted in Louisania by the biologists engaged by oil companies and by persons representing various conservation and fishery interests have not been published and are not generally available. They are probably rather limited since these investigators have not been

prepared to give consistent attention to the studies of diatoms and were primarily concerned with other problems. Mention may be made here of the observation by Willis Hewatt of Texas Christian University (personal communication) that *Biddulphia mobilensis* periodically produces very heavy concentrations off the Louisiana coast near Grand Isle. This area, and probably also the coasts of Alabama to Texas, would seem to be optimum environment for this species.

DIATOM FLORAS OF GULF AND ADJACENT WATERS

At the present state of our knowledge there is no basis for correlating diatom floras of the Gulf and adjacent areas or for discussing their mutual effects. Currents that swing into the Gulf from the Caribbean on the southeast and out through the Florida Straits on the northeast must, of course, carry their complement of plankton diatoms; but, until more is known of both the Gulf diatom flora and that of the adjacent waters outside, no definite information can be given regarding the effect of one on the other. As has been said, practically nothing is known specifically of the Gulf diatom plankton or, for that matter, of that in adjacent tropical waters.

The mere presence of similar population constituents in the adjacent areas does not necessarily imply any direct relationship between them. It is quite possible that the greater sweep of the Gulf Stream tends to some extent to isolate the Gulf of Mexico from the adjacent seas despite the movement of some of the Atlantic and Caribbean waters through the Gulf.

With the bottom-living and attached species seemingly not so readily subject to dispersion, there is not enough difference of conditions, say, on the east and west coasts of Florida or the environs of Cuba, and there is so much correspondence in certain conspicuous species, such as *Terpsinöe musica*, *T. americana*, *Nitzschia paradoxa*, *Grammatophora marina*, *Biddulphia pentacrinus*, *Raphoneis surirella*, *Surirella reniformis*, and members of the genera *Coscinodiscus*, *Campylodiscus*, *Biddulphia*, *Navicula*, that in our present state of limited knowledge it is not feasible to give any general statements of significant relationship. It would seem that a very large variety of species find the waters both inside and outside the Gulf a suitable habitat, but it will take a great deal of more detailed collecting and comprehensive study to disclose any significant floristic differences or migrational influences within these areas.

ECOLOGY

The literature on the diatoms of the Gulf area contains practically nothing concerning their ecology and economic importance. The designation of species as fresh water, brackish, or marine is about the extent of ecological data. Yet, both subjects should be of great interest. One may expect that careful studies of many diverse habitats represented along the shorelines of the Gulf, and in its open waters could give valuable data regarding habitat characteristics, optimal range of the different species, and their seasonal occurrences.

The effects of the discharge of particulate matter by the Mississippi and other large rivers on the distribution and productivity of diatoms in the open waters constitutes another important problem.

Relation of the diatoms as a vital chain in the marine food cycle is also of great interest because of the extensive shrimp, oyster, and fishery industries of the area.

Such ecological studies of the diatoms correlated with their floristic survey may well contribute to general knowledge of the Gulf and will be helpful in understanding its specific problems.

PRODUCTIVITY

It has long been held that productivity of plankton diatoms in tropical and subtropical waters is in general lower than in colder regions. This, in the writer's experience, appears to be generally true, but the statement should be taken with some qualifications for there are instances in which, owing to a particular combination of local conditions, it does not hold. Even in tropical waters certain areas may contain heavy concentrations of diatoms. There is for instance evidence of occasional unaccountable surges of certain species, as *Hemidiscus*, *Biddulphia mobilensis* and *Isthmia capensis* about Tortugas and in other places for which the causative factors are not known. Because of the presence of very delicate, transparent and minute forms that pass through the meshes of the plankton net, the Gulf plankton may at times contain a greater number of individual diatoms and be more productive than

meets the eye of the casual observer. Examples of such occurrences are given in the next section on silica relations. Although a phytoplankton tow in the very clear subtropical Gulf water will usually disillusion and disappoint the investigator used to northern collecting, he must be alert both in observation and method not to miss or lose the delicate and minute forms present.

The first adequate quantitative studies of diatom plankton productivity in the Gulf were made at Tortugas by Riley (1938). His work, based on Harvey's method of extraction of plankton pigments, and on measurements of oxygen changes in suspended clear and dark bottles (method of Marshall and Orr), gives indices of reliable value. It might be added that, especially with the phantom-like diatom plankton, these methods are dependable, while errors and uncertainties of sampling with quantitative plankton net and of cell counts would give deceptive results.

Comparing plankton productivity at Tortugas with that of Long Island Sound, Riley found that the amount of total plant pigment from Tortugas plankton was only one twenty-fifth that of the Long Island area. On the other hand, oxygen production in suspended bottles was one-third to one-half as much in the former as in the latter area. It would seem evident, he says, "that actual productivity is much greater than the standing crop would indicate." The results are subject to qualification with respect to a number of altering factors which are discussed in Riley's report.

The limited period covered by Riley's observations may or may not have been a favorable one for comparison, and further investigations of this character extended to other places in the Gulf and other times of the year, are clearly needed.

Another problem about which information to date is both meager and vague concerns the rate of turnover and renewal of the population, especially of the small diatom species such as members of the genera *Nitzschia, Synedra, Dimmerogramma, Grammatophora, Amphora, Raphoneis.* The estimation of the so-called "standing crop" of phytoplankton growth is a standard and fairly satisfactory practice, but an adequate evaluation of the amount of transformation of organic substance over a specified period of time is fraught with a complication due to the constant breakdown and renewal of population elements, in which the reproductive rate is rapid and the life span is short. Especially is this true where the plankton is very poor as it is frequently in the Gulf waters.

Knowledge of the general occurrence and succession of the Gulf flora is too meager to make any reliable statements as to the relative importance of the various diatoms for there are very many of the species mentioned, and perhaps others, that occur at times in large numbers. Just a few, however, that are definitely typical of the region, though by no means restricted to it might be cited: *Biddulphia mobiliensis* (Bail.) Grun., *Terpsinöe musica* Ehr., and *Hemidiscus hardmannianus* (Grev.) Mann. Further study will certainly add many others that periodically occur in abundance in different parts of the area.

SILICA RELATIONSHIPS

In the waters of tropical seas, poor in silica and other nutrients, the diatoms of wide or cosmopolitan distribution are smaller and have frailer shells than are to be found in the same species from waters of temperate and northern latitudes. The variety of species is not less in the tropics, nor is there necessarily a smaller number of individuals, but the size and robustness of their cells is diminished. Although this observation is applicable, in general, to species found both in tropical and in temperate seas, certain forms may be cited as notable examples, namely, *Synedra undulata* (tropical form often half the length of its northern counterpart), *Biddulphia pulchella* and *B. pentacrinus, Surirella reniformis, Grammatophora marina, Isthmia* sp., and others. On the contrary, some typically warmer water forms, like *Raphoneis surirella* do not appear to grow larger, heavier shells in richer waters of northerly latitudes.

The plankton diatoms of the waters containing minimum amount of dissolved silica are diaphanous, as for example, the *Chaetoceros*, large-celled *Hemidiscus* and *Coscinodiscus* species found in the Gulf plankton. These latter, and similar forms, may be both large and numerous, but their bodies are so watery and their shells so lightly silicified that they are very transparent and are easy to overlook.

Numerous minute-celled forms such as small *Nitzschia, Cocconeis, Dimmerogramma, Synedra, Grammatophora,* and *Amphora* species, common in

the Gulf frequently are found in silica poor waters, while larger heavy-shelled forms (*Rhizosolenia, Coscinodiscus, Biddulphia* sp.) sometimes found in cooler, northern waters, are not present in the tropical or subtropical plankton unless reduced in size or weight of their silica shells. These observations are general and at present not based on extensive quantitative measurements which, however, are being planned by the author.

Further observations by the writer, although not quantitative, strongly suggest that wherever there is a substantial influent of silica-bearing water, the diatom growth is both more abundant, and the cells (and their shells) are of a more robust character. Such a condition was noticed, for instance, at Tortugas in close proximity to the crumbling walls of siliceous brick of old Fort Jefferson, washed on all sides by the shallow calcareous water. In the moat and in semienclosed pools adjacent to these walls a very heavy growth of *Tropidoneis lepidoptera* and other diatoms was noted. The more extensive result of such relations, however, is to be seen in areas influenced by the discharge of river systems that drain argillaceous soils, or in the inshore waters affected by the run-off from steeper siliceous terrain, such as found around the coast of Cuba, the west coast of Florida and the coast of Alabama. Waters of such constitution support heavy growths of robust shelled diatoms as *Terpsinöe musica, Biddulphia pulchella, Hydrosera triquetra, Lithodesmium*, and others.

The contrast of the rich diatom flora produced in such an environment with the frail and delicate plankton forms of the silica-poor calcareous waters about Tortugas, for example, appears to be a demonstration of a point long suspected by the writer that a plentiful supply of silica greatly enhances the growth of diatoms. Evidence from other regions and types of habitat, in the writer's experience, supports this contention. Where richer waters with a higher silica content occur in tropical regions owing to cold currents, upwelling, or run-off from siliceous soils, a heavy diatom productivity, with oftentimes more robust individuals is the result.

The relation of diatom growth to silica content of sea water is undoubtedly significant but not too well understood. The varied conditions of the Gulf of Mexico afford good opportunity for such study. The effects of phosphates, nitrates, and other nutritive elements should be examined coordinately although it does not appear from the present observations that they could be confused with the role of silica as a limiting factor.

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CHAPTER VII
PROTOZOA

GULF OF MEXICO FORAMINIFERA

By FRED B. PHLEGER and FRANCES L. PARKER,[1] *The Scripps Institution of Oceanography, University of California*

Foraminifera are relatively large, marine Protozoa having either a calcareous or an arenaceous test; they are both benthonic and planktonic in habitat. Their tests contribute a large percentage of the material in marine sediments. Study of Foraminifera has been mostly confined to the occurrence of empty tests in marine sediments, and all identifications are based upon test morphology.

Little is known of Gulf of Mexico Foraminifera except from the Dry Tortugas and from the northwest area. Phleger (1951) and Phleger and Parker (1951) have studied living and dead assemblages from plankton tows and cores taken off shore between Point Isabel and Atchafalaya Bay, and the present report is largely a summary of the pertinent features of that work. These samples were collected from 551 stations spaced in 12 traverses extending from the 10-fathom curve to the center of the Sigsbee Deep. Flint (1899) and Cushman (1918–31) have described material collected by the United States Bureau of Fisheries ship, *Albatross*, from the northern part of the Gulf of Mexico east of the Mississippi Delta. Kornfeld (1931) described some shallow-water and littoral Foraminifera from a few stations between the Mississippi Delta and the International Boundary. Cushman and Bermudez (1945) reported a new species of *Rotalia* from the mouth of the Rio Grande. Cushman (1922) has described numerous species from the shallow-water areas of the Tortugas.

BENTHONIC FORAMINIFERA

The area investigated in the northwest Gulf of Mexico between the Mississippi Delta and the International Boundary is one of clastic sediments. Clastic sediments also occur east of the delta as far as Mobile Bay and along the coast of Mexico. The continental shelf bordering Louisiana and Texas has numerous isolated calcareous reefs. The principal calcareous areas in the region are along the coasts of Florida and Yucatán. The Foraminifera assemblages in these two sedimentary environments are quite distinctive and are treated separately in the following summary. The most extensive sampling and study has been done in the clastic sediments.

Clastic areas.—Figures 55 through 58 list the principal benthonic species found in the northwest Gulf of Mexico; this figure is reproduced from Phleger (1951). The depth range shown for each species is a generalization based upon distributions from samples in all 12 traverses taken. This assemblage is related to the Atlantic assemblage but contains some elements reported only from the Gulf of Mexico.

The benthonic faunas in the northwest Gulf may be grouped into six depth biofacies with boundaries at the following approximate depths: 100 m., 200 m., 600 m., 1,000 m., and 2,000 m. In addition, there are three subfacies in the upper 100 m. of water depth. The boundaries between these biofacies are not sharp but vary through about 10–20 percent of the depth involved. Figure 59 summarizes the depth of biofacies and gives depth ranges of representative species as an illustration of the basis for distinguishing the facies.

The most striking depth biofacies boundary in this area is at about 100 m. This coincides with the depth of the water layer which is affected by changing seasons and therefore shows seasonal temperature ranges, in which the greatest organic production occurs, and which is turbulent, at least in part. Deeper biofacies boundaries may be correlated with the temperature ranges if they occur in the permanent thermocline. The boundary at about 2,000 m. is believed to be due to some environmental factor other than temperature, since there is no significant temperature change

[1] Contribution from the Scripps Institution of Oceanography, New Series No. 660, Contribution No. 16, Marine Foraminifera Laboratory. Work done on Office of Naval Research Project NR 081 050.

FIGURE 55.—Generalized depth ranges of benthonic Foraminifera in the Gulf of Mexico. Solid lines indicate relatively greater abundance than dashed lines.

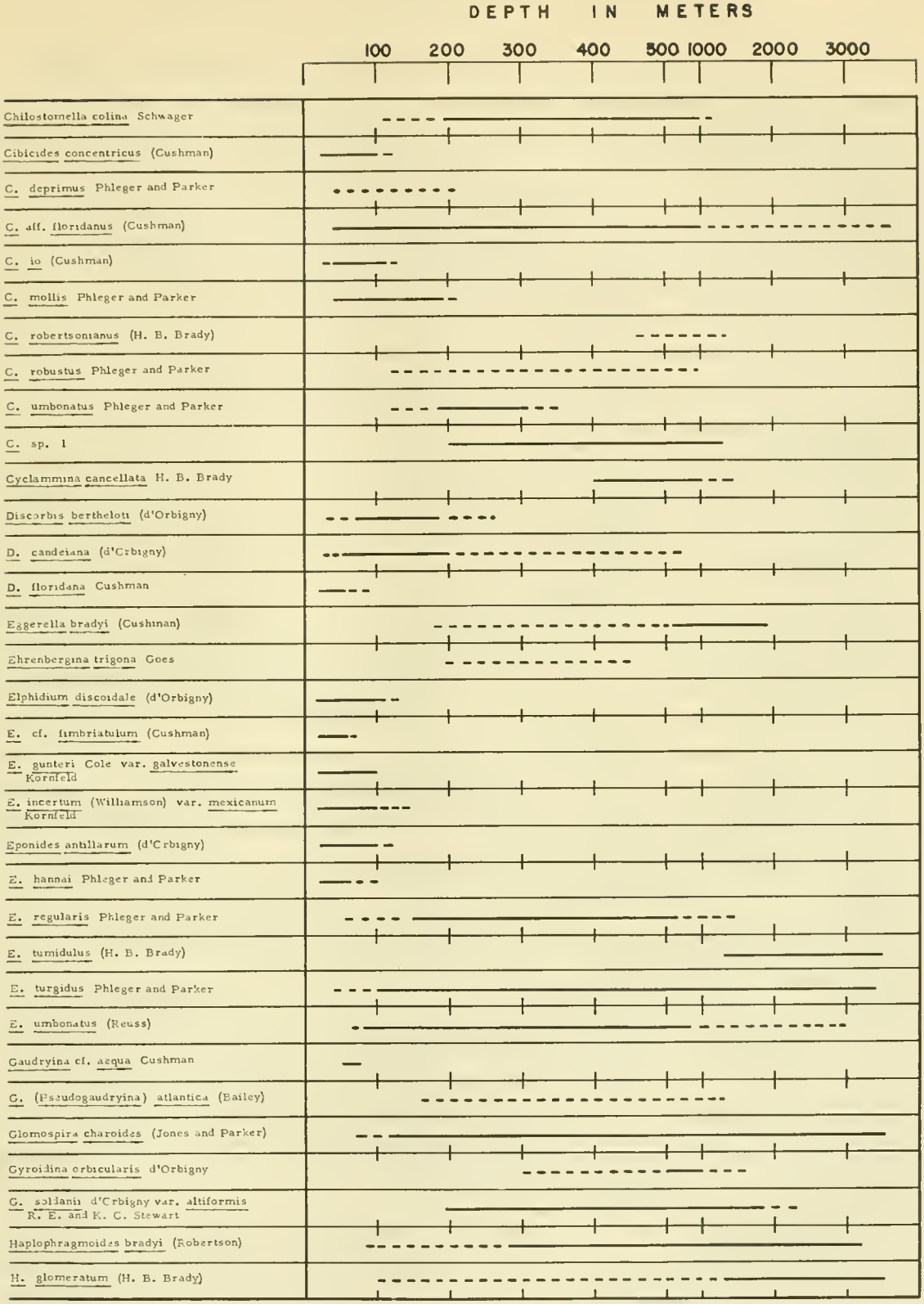

FIGURE 56.—Generalized depth ranges of benthonic Foraminifera in the Gulf of Mexico. Solid lines indicate relatively greater abundance than dashed lines.

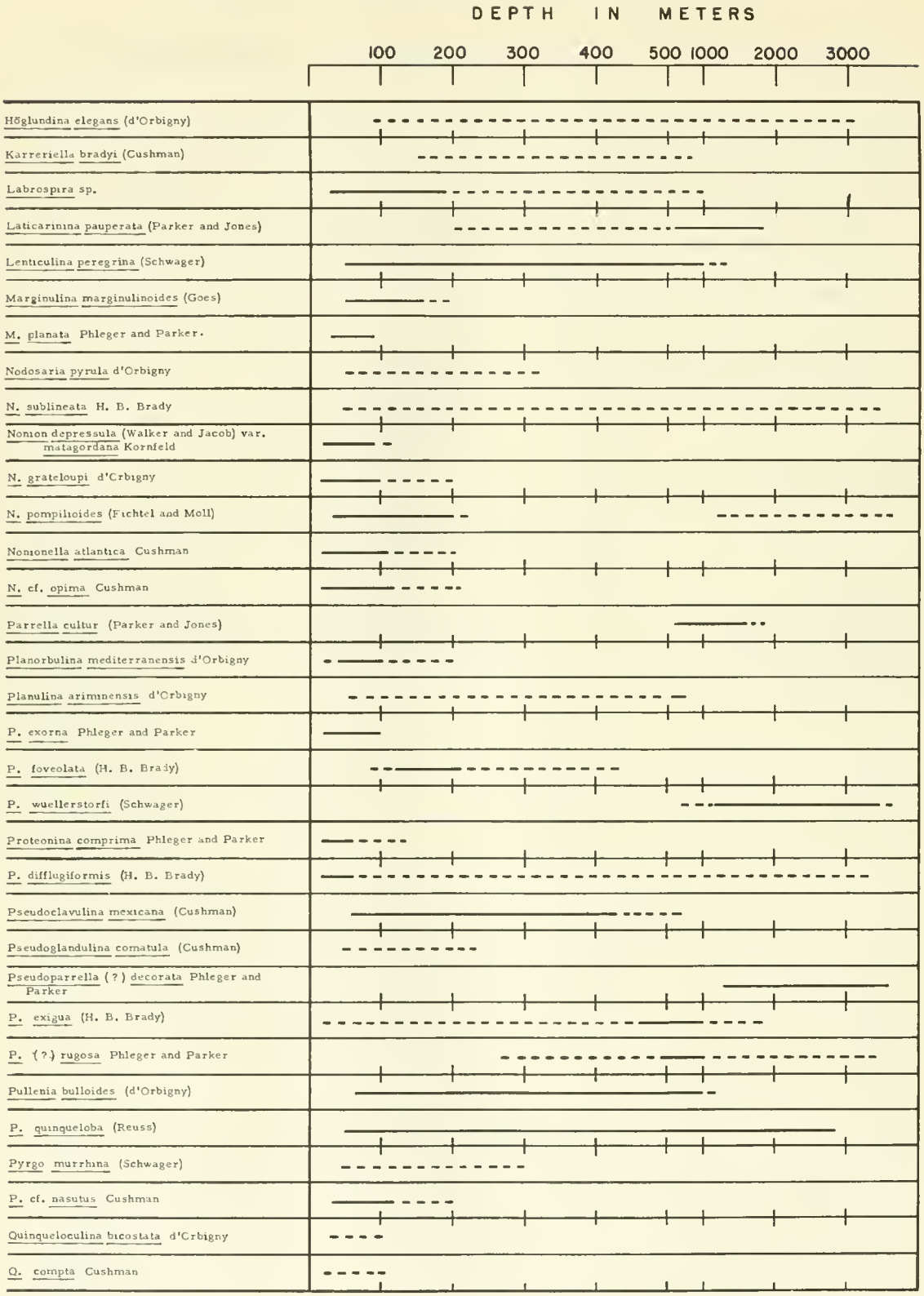

FIGURE 57.—Generalized depth ranges of benthonic Foraminifera in the Gulf of Mexico. Solid lines indicate relatively greater abundance than dashed lines.

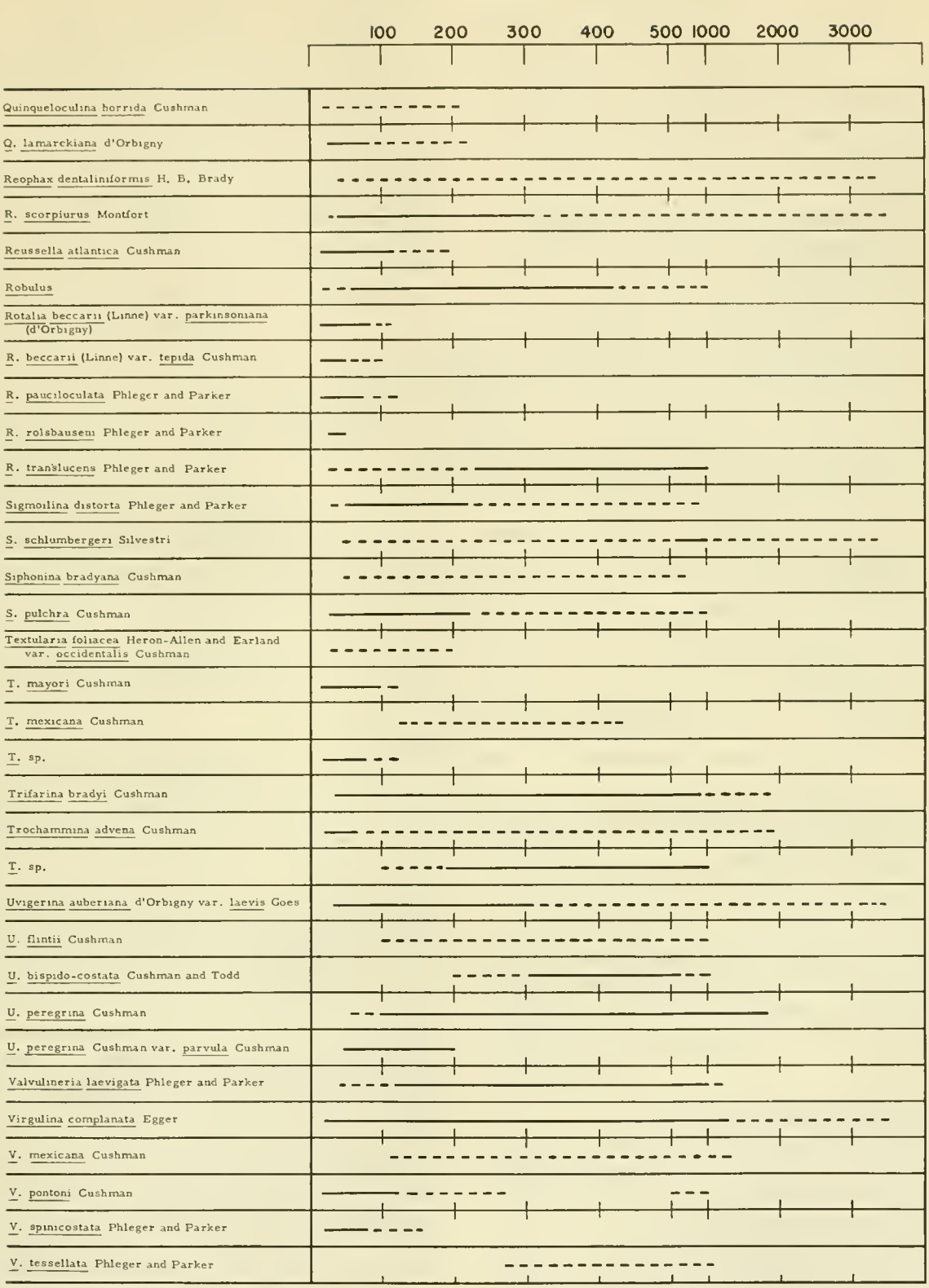

FIGURE 58.—Generalized depth ranges of benthonic Foraminifera in the Gulf of Mexico. Solid lines indicate relatively greater abundance than dashed lines.

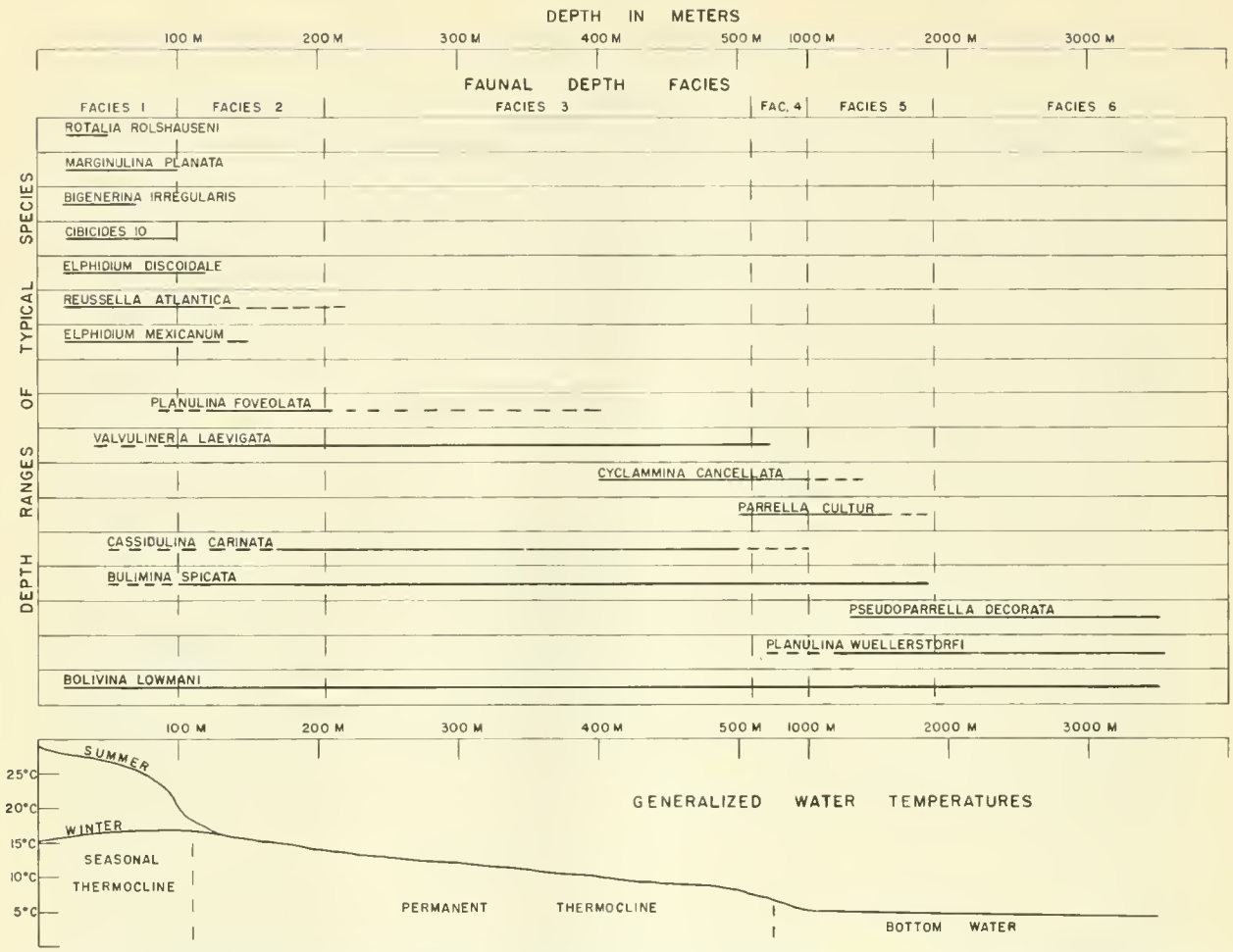

FIGURE 59.—Generalized chart showing depth biofacies of benthonic Foraminifera in the Gulf of Mexico and correlation between depth biofacies and temperature. Depth range lines are of benthonic Foraminifera used to illustrate types of depth distributions found.

below the bottom of the permanent thermocline at about 800–1,000 m.

Living specimens have been collected of 78 benthonic species. The greatest number of living specimens were found of the following species, all of which are characteristic of the facies above 100 m.:

Bifarina advena (Cushman).
Bolivina lowmani Phleger and Parker.
B. striatula Cushman var. *spinata* Cushman.
Buliminella cf. *bassendorfensis* Cushman and Parker.
Cancris oblonga (Williamson).
Cibicides concentricus (Cushman).
Elphidium discoidale (d'Orbigny).
Nonionella atlantica Cushman.
Proteonina comprima Phleger and Parker.
Rotalia beccarii (Linné).
Virgulina pontoni Cushman.

The highest production rate of benthonic Foraminifera is in the upper facies, although the largest population of accumulated empty tests in bottom sediments usually is at intermediate depths.

Calcareous areas.—The Foraminifera fauna of the calcareous areas is quite distinctive from that of the clastic areas and is dominated by *Amphistegina lessonii* d'Orbigny, a typical calcareous species.

Cushman (1922) described the Foraminifera from several environments of the Dry Tortugas area off the southwest coast of Florida. The sampling was too scattered to give dependable results of the distribution in these environments, some being represented by only one or two stations. For this reason, the following description

includes only the outstanding characteristics of the area.

The area sampled is in shallow water with a maximum depth of 33 m. but chiefly 20 m. or less. The bottom sediment at the majority of stations is described as "fine white sand" or "sand"; this is calcareous sand. The fauna closely resembles that of the general West Indies region which, in turn, is similar to the warm, shallow faunas of the Indo-Pacific. Cushman described about 150 species from the area. The following list includes many of the most widely distributed and common species described:

Amphistegina lessonii d'Orbigny.
Archaias angulatus (Fichtel and Moll).
A. compressus (d'Orbigny).
Asterigerina carinata d'Orbigny.
Bigenerina irregularis Cushman and Parker.
Bolivina pulchella (d'Orbigny).
Cymbalopora squammosa (d'Orbigny).
Discorbis candeiana (Cushman).
D. mira Cushman.
D. subaraucana Cushman.
Elphidium discoidale (d'Orbigny).
E. poeyanum (d'Orbigny).
Triloculinella circularis (Bornemann).
Nonion grateloupi (d'Orbigny).
Pyrgo subsphaerica (d'Orbigny).
Quinqueloculina agglutinans d'Orbigny.
Q. lamarckiana d'Orbigny.
Q. laevigata d'Orbigny.
Rotalia rosea (d'Orbigny).
Spiroloculina antillarum d'Orbigny.
Textularia agglutinans d' Orbigny.
T. candciana d' Orbigny.
Triloculina rotunda d'Orbigny.
Virgulina punctata d'Orbigny.

The *Amphistegina* fauna also is reported from an isolated calcareous reef area in the northwest Gulf of Mexico.

PLANKTONIC FORAMINIFERA

Planktonic Foraminifera are abundant in offshore areas of the northwest Gulf of Mexico off the continental shelf both as accumulations of tests in the sediments and as living members of the planktonic population. Occasional concentrations of planktonic specimens are found in shallow water. The planktonic fauna is dominated by great abundance of *Globigerinoides rubra* (d'Orbigny) and contains the following additional species in the surface bottom sediments:

Candeina nitida d'Orbigny.
Globigerina bulloides d'Orbigny.
G. eggeri Rhumbler.
G. inflata d'Orbigny.
Globigerinella acquilateralis (H. B. Brady).
Globigerinoides conglobata (H. B. Brady).
G. sacculifera (H. B. Brady).
Globorotalia menardii (d'Orbigny).
G. punctulata (d'Orbigny).
G. scitula (H. B. Brady)
G. truncatulinoides (d'Orbigny).
G. tumida (H. B. Brady).
Orbulina universa d'Orbigny.
Pulleniatina obliquiloculata (Parker and Jones)
Sphaeroidina bulloides d'Orbigny.
Sphaeroidinella dehiscens (Parker and Jones).

Living specimens of all but 6 of these species have been found in serial plankton tows taken from various depths of water at 27 stations occupied during February and March 1947. The average living planktonic Foraminifera population from these samples is about 5–6 specimens a cu. m. of water at 25–50 m. water depth, and much larger shallow-water populations are found in certain localities. Living specimens were collected at all depths of water sampled down to about 1400 m., but the largest population is in the upper layers at most stations. At a few stations there was a larger population collected at considerable depth than from near the surface. Nine specimens of planktonic Foraminifera, comprising six species, were found living on the surface of the bottom sediments.

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PROTOZOA [1]

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The Protozoa considered here include all the orders recognized by Pearse (1949) excepting Dinoflagellata and Forminifera,[2] these two groups being so abundantly represented in the Gulf of Mexico and relatively so well-known that they are given separate treatment. Nothing which is said below, therefore, is to be construed as applying to those orders excepting when they are specifically mentioned. An attempt has been made to list in this paper every protozoan which has been reported from the Gulf. Although it is believed that most of the important papers have been reviewed, it is quite possible that some of them have been overlooked.

The number of species in any particular order which have been recorded in the literature pertaining to the Gulf does not by any means give an indication of the extent to which that order is actually represented there, since relatively only a very few studies on Protozoa of the Gulf of Mexico have been conducted. When each order is considered below, therefore, not only are the reported species (if any) listed but a statement is usually made to indicate whether or not an investigator would expect to find numerous representatives of that group living under the conditions existing in the Gulf. For instance, one would not expect to find in the marine habitats many representatives of Euglenoidina or Heliozoa, which are predominantly fresh water forms, or members of Hypermastigina, which are exclusively inhabitants of the alimentary canal of certain land dwelling insects. On the other hand, such orders as Radiolaria, which are exclusively marine, and Microsporidia, which are common parasites of invertebrates and lower vertebrates living in almost any conceivable habitat, are probably very abundantly represented both in variety of species and numbers of individuals.

To anyone interested in Protozoa of the Gulf of Mexico there is a striking contrast between the apparently limitless variety of species there and the very scant attention which protozoologists have given them. The semitropical climate and the great diversity of habitats found in the Gulf proper and its contiguous waters undoubtedly provide suitable environments wherein a corresponding diversity of species of free-living protozoan fauna not only are able to live but can reproduce rapidly and flourish. The same favorable conditions give rise, also, to a great abundance and variety of other invertebrates and fishes which serve as hosts of protozoan parasites. Numerous species of the parasitic Protozoa not only find suitable hosts, but the relatively high temperatures of the southern waters are accompanied by rapid multiplication of these parasites and, consequently, their occurrence in great abundance. Although several of the species of Protozoa reported to occur in the Gulf were previously known ones, the overwhelming majority have been new. This fact alone suggests that any serious investigator would be richly rewarded for his efforts by many discoveries. The Protozoa of the Gulf of Mexico, both free-living and parasitic, constitute one of the great American frontiers in protozoology. A few individuals have probed its fringes, but its thorough exploration is a task for future investigators to undertake.

SURVEY OF THE LITERATURE

The known Protozoa of the Gulf of Mexico (exclusive of Dinoflagellata and Foraminifera) are mostly free-living amoebae, ciliates (both free-living and parasitic), and Sporozoa. The first two groups have been studied chiefly along the Florida coast and the third along the coasts of Texas, Louisiana, and Mississippi, especially at Louisiana State University Marine Laboratory located on

[1] The writer is indebted to Paul S. Galtsoff and Harold W. Harry for invaluable aid in obtaining pertinent literature and to Sewell H. Hopkins for criticism of one portion of the manuscript.

[2] See articles by H. W. Graham, Dinoflagellates of the Gulf of Mexico, pp. 223–226 of this book, and by F. B. Phleger and F. L. Parker, Gulf of Mexico Foraminifera, pp. 235–241.

Grand Isle, La. Jacobs (1912) made physiological studies on four unidentified species of ciliates infesting sea urchins in the vicinity of the former Biological Laboratory of Carnegie Institution at Dry Tortugas, a group of islands located approximately 60 miles west of Key West, Fla. Powers (1933 and 1935) studied about 13 species of ciliates (including those observed by Jacobs) at Tortugas, describing and naming 6 new ones. He described, also, one new flagellate. More recently, Wichterman (1940, 1942, and 1942a) described 3 new ciliates from an oligochaete and 1 on coral, all at Tortugas. He observed in the same oligochaete host an unidentified gregarine. Bullington (1931, 1935, 1939, 1939a, and 1940) made a series of studies on 15 free-living ciliates at Tortugas, a dozen of which were new species, and observed many unidentified ones as well. Noland (1937) studied 18 species of free-living ciliates, 6 of which were new, at Bass Biological Laboratory, Englewood, Fla. Schaeffer (1926) has been the chief student of the amoebae. He made a series of studies which culminated in a lengthy paper on taxonomy of the amoebae with description of 23 (?) new species from Tortugas and Key West, Fla. Hopkins (1931) made life history studies on 2 of the same amoebae at Tortugas and 1 mycetozoan. Apparently, Prytherch (1938, 1940) made the first noteworthy observations on a sporozoan of the Gulf of Mexico. He observed *Nematopsis* in oysters from Lake Barre and vicinity in Louisiana to Mobjack Bay, Va., and described the first member of the genus known in American waters. Later, Sprague (1949, 1950, 1950a, and this paper) studied 7 sporozoan parasites, 6 of them new, of mollusks and decapod Crustacea along the Louisiana coast. Mackin et al. (1950) described a sporozoan (?) parasite, *Dermocystidium marinum*,[3] of widespread occurrence in oysters along the Gulf coast. Most of the other Protozoa considered here have been mentioned only casually in the literature or called to the attention of the writer in personal correspondence.

DISTRIBUTION OF PROTOZOA

Most of the known Protozoa of the Gulf of Mexico have been reported as new species. These and the previously known ones have usually been reported only from particular localities. Not much about their general distribution, therefore, seems to be known. We may reasonably suppose, however, that certain generalizations about distribution of free-living Protozoa elsewhere in the world may give us some idea about the expected distribution of those known in the Gulf since particular species generally tend to occur wherever the particular conditions favoring their life processes exist. Pertinent remarks on distribution of free-living forms can be found in Calkins' (1933, pp. 25–26) book on biology of Protozoa.

The distribution of parasitic Protozoa is necessarily limited to that of their hosts. The hosts themselves are not generally so widely distributed as are the free-living Protozoa, one reason being, perhaps, that the means of dispersal available to them are somewhat more limited. Furthermore, distribution of parasitic Protozoa is not necessarily so extensive as that of their hosts, since environmental conditions tolerated by the latter may be unfavorable to the former. Protozoa with alternation of hosts (such as many of the Sporozoa) are further limited in distribution, since the definitive and intermediate hosts, both necessary for survival of the parasite, may not have the same range of adaptability to different habitats. While the host species living in geographical isolation have been undergoing evolutionary divergence their parasites have likewise diverged to give rise to separate varieties and species. In view of these considerations, the parasitic Protozoa occurring in the Gulf of Mexico are less likely to be identical with species found in similar habitats elsewhere than are the free-living ones. To phrase the same idea in positive terms, one would expect, a priori, to find that many of the parasitic Protozoa in the Gulf of Mexico are new ones. The limited information we have about them, in fact, tends to support that conclusion, since the overwhelming majority of them have been previously unrecorded species. The noteworthy exceptions were some of the ciliates observed by Powers (1935) in sea urchins; about half of them had previously been described at Bermuda and Beaufort, North Carolina. With one or two exceptions, as far as the writer knows, each of the parasitic species known in the Gulf of Mexico has been observed only in one or few

[3] Taxonomic position of *Dermocystidium* was rather uncertain. In 1952 Ray found that this microorganism is a fungus (Ray, Sammy M., 1952, A Culture Technique for the Diagnosis of Infections with *Dermocystidium marinum* Mackin, Owen and Collier, in Oysters, Science 116: 360–361).

localities, and little attempt has been made to determine the extent of distribution. The exceptions are *Nematopsis ostrearum* and *Dermocystidium marinum* (see footnote, p. 244), both parasites of the oyster *Crassostrea virginica*. Although much information accumulated by numerous investigators relative to these two parasites remains unpublished, a comprehensive report by Landau and Galtsoff (1951) on the Distribution of *Nematopsis* has recently appeared. Since little can be said positively about the distribution of parasitic Protozoa in general, and those in the Gulf of Mexico in particular, this is a subject full of promise for future study. It would be of particular interest, from the economic point of view, to add to our meager information more data on the distribution of the protozoan parasites of such commercially important seafood animals as the shrimp, crabs, and oysters.

Subphylum 1 PLASMODROMA Doflein 1901

Class 1 MASTIGOPHORA Diesing 1865

Subclass 1 *Phytomastigina* Doflein 1916

The Phytomastigina include those flagellates in which the plant characteristics are either predominant or clearly marked. Of the six orders, two (Phytomonadina and Euglenoidina) are predominantly freshwater forms commonly considered to be Algae as well as Protozoa, one (Chloromonadina) consists of rare and little known flagellates, another (Dinoflagellata) is so prominently represented in the Gulf that it is given separate treatment, and the other two (Chrysomonadina and Cryptomonadina) are commonly represented in salt water, but the writer knows of practically no reports on them from the Gulf. The Phytomastigina are, therefore, given very little consideration here.

Order 1 CHRYSOMONADINA Stein 1878

Although the Silicoflagellidae are exclusively marine plankton, and the Coccolithidae are mostly marine, the writer is not familiar with reports of members of this order from the Gulf of Mexico.

Order 2 CRYPTOMONADINA Stein 1878

"The Cryptomonadina occur in fresh or sea water, living also often as symbionts in marine organisms." (Kudo, 1946, p. 213).

Suborder 1 EUCRYPTOMONADINA Pascher 1913

Family CRYPTOMONADIDAE Stein

1. Chilomonas (?).

This organism was observed by Pearse (1932) in a brackish water pool (Pool 5) at Garden Key, Tortugas.

Order 3 PHYTOMONADINA Blochmann 1895

These are mostly fresh water Algae.

Order 4 EUGLENOIDINA Bütschli 1884

Members of this order are likewise mostly fresh water Algae.

Order 5 CHLOROMONADINA Klebs 1892

"The chloromonads are of rare occurrence and consequently not well known." (Kudo, 1946, p. 243.)

Order 6 DINOFLAGELLATA Bütschli 1885

The dinoflagellates, which include many well-known planktonic forms in the Gulf, are treated separately (pp. 223–226).

Subclass 2 *Zoomastigina* Doflein 1916

The majority of this subclass are either parasitic in land dwelling or fresh water animals or free living in fresh water.

Order 1 RHIZOMASTIGINA Bütschli 1883

Although some members of this group occur in salt water, the writer is not aware of reports of any of them from the Gulf of Mexico.

Order 2 PROTOMONADINA Blochmann 1895

Organisms belonging definitely to this order seem not to have been reported from the Gulf. However, certain trypanosomelike organisms (now generally regarded as spirochaetes) very commonly occur in the intestinal tracts, especially in the crystalline styles, of various lamellibranch mollusks in many parts of the world. It is common knowledge among oyster biologists that they occur in oysters of the Gulf, although no one seems to have recorded the fact. Those organisms are mentioned here for lack of a better place to consider them. Dimitroff (1926) made an intensive study of the spirochaetes of Baltimore market oysters. He gave a complete review of the literature and listed 11 species or varieties which he found. He assigned 4 of the types to *Saprospira* Gross, 1910, and 7 to *Cristispira* Gross, 1910. Possibly the spirochaetes of Gulf coast oysters,

when identified, will be found to be similar to those studied by Dimitroff.

Order 3 POLYMASTIGINA Blochmann 1895

Suborder 1 MONOMONADINA Kudo 1939

Family CHILOMASTIGIDAE Wenyon

1. *Chilomastix echinorum* Powers, 1935.

In intestinal ceca of the sea urchin, *Tripneustes esculentus*. Discovered by Powers (1935) in the vicinity of Bird Key, Tortugas.

Class 2 SARCODINA Hertwig and Lesser 1874

Subclass 1 *Rhizopoda* von Siebold 1845

Order 1 PROTEOMYXA Lankester 1885

The writer is not familiar with reports of representatives of this group in the Gulf.

Order 2 MYCETOZOA de Bary 1859

1. A mycetozoan. Hopkins (1931) made observations on an unidentified mycetozoan at Tortugas.

Order 3 AMOEBINA Ehrenberg 1830

The principal report on the amoebae of the Gulf which has come to the attention of the writer is Schaeffer's (1926) lengthy paper on taxonomy of the amoebae. He described a number of new species from Key West and Tortugas and proposed an extensive revision of the nomenclature of the free-living amoebae. As Hyman (1940) has pointed out, Schaeffer's terminology has not been generally accepted. Nevertheless, the nomenclature of this group has remained unsettled and has given rise to a considerable body of literature which was recently reviewed briefly by King and Jahn (1948). For the sake of convenience, Schaeffer's terminology is followed here in listing the species he reported. This is not intended to imply that the writer holds any opinion concerning the taxonomy of the group.

Family CHAIDAE Poche

1. *Trichamoeba sphaerarum* Schaeffer, 1926.

Schaeffer (1926) observed this amoeba in towings and upon floating seaweed. He found it to be a common species in the vicinity of Tortugas.

2. *Trichamoeba pallida* Schaeffer, 1926.

Schaeffer (1926) easily obtained this organism in Tortugas by letting a small stream of sea water filter through a small wad of cotton for a few days.

3. *Metachaos fulvum* Schaeffer, 1926.

Found by Schaeffer (1926) in irrigated cultures in Tortugas.

Family MAYORELLIDAE Schaeffer

4. *Flabellula mira* Schaeffer, 1926.

According to Schaeffer (1926, p. 48), found in Key West, Tortugas, and Cold Spring Harbor, Long Island, among blue-green algae. Hopkins (1931) studied the life history of this amoeba at Tortugas.

5. *Flabellula citata* Schaeffer, 1926.

Schaeffer (1926) saw this amoeba in salt water at Tortugas, at Cold Spring Harbor, and at Casco Bay, Maine. Hopkins (1931) studied, also, the life history of this amoeba at Tortugas.

6. *Flabellula crassa* Schaeffer, 1926.

Discovered by Schaeffer (1926) in irrigated sea water cultures in the laboratory at Tortugas.

7. *Flabellula pellucida* Schaeffer, 1926.

In describing this species Schaeffer (1926, p. 54) stated that this marine amoeba was found with blue-green algae from Key West harbor, Florida. His tabulation of species (p. 22) indicates that it was found at Tortugas.

8. *Mayorella conipes* Schaeffer, 1926.

Found by Schaeffer (1926) at Tortugas and at Long Island Sound and Great South Bay, Long Island.

9. *Mayorella gemmifera* Schaeffer, 1926.

According to Schaeffer's (1926) description (p. 50), this organism was observed both at Tortugas and Cold Spring Harbor. His tabulation (p. 22), however, indicates that it was found only at Tortugas where it was collected by running sea water through cotton.

10. *Mayorella crystallus* Schaeffer, 1926.

Discovered by Schaeffer (1926) in salt water aquaria in the laboratory at Tortugas.

11. *Vexillifera aurea* Schaeffer, 1926.

Found by Schaeffer (1926) in salt water aquaria at the laboratory at Tortugas and also at Cold Spring Harbor.

12. *Striolatus tardus* Schaeffer, 1926.

Schaeffer (1926) stated (p. 26) that this amoeba was collected with blue-green algae in shallow water near a dock at Key West harbor. His table (p. 22) indicates that it was found at Tortugas.

13. *Dactylosphaerium acuum* Schaeffer, 1926.

Found by Schaeffer (1926) among blue-green algae in very shallow water at Key West harbor and also in salt water aquaria in the laboratory at Tortugas.

14. *Pontifex maximus* Schaeffer, 1926.

Schaeffer (1926) discovered this species in cultures from Casco Bay, Maine, and observed it, also (p. 22) in Tortugas.

Family THECAMOEBIDAE Schaeffer

15. *Rugipes vivax* Schaeffer, 1926.

Schaeffer (1926) collected this species at Tortugas and in tidal pools at Cold Spring Harbor.

16. *Thecamoeba orbis* Schaeffer, 1926.

This amoeba was discovered by Schaeffer (1926) on floating seaweeds in the vicinity of Tortugas, and it was also seen at Cold Spring Harbor.

17. *Thecamoeba munda* Schaeffer, 1926.

Found by Schaeffer (1926) among blue-green algae in Key West harbor and in cultures of seaweeds from Tortugas.

18. *Thecamoeba hilla* Schaeffer, 1926.

Found by Schaeffer (1926) in cultures in the laboratory at Tortugas and in Cold Spring Harbor.

19. *Thecamoeba rugosa* Schaeffer, 1926.

Found by Schaeffer (1926) among blue-green algae at Key West harbor, in a salt water tank in the laboratory at Tortugas, and at Cold Spring Harbor.

Family HYALODISCIDAE Poche

20. *Unda maris* Schaeffer, 1926.

Schaeffer (1926) discovered this amoeba in the salt water tank in the laboratory at Tortugas.

21. *Gobodiscus gemma* Schaeffer, 1926.

Found by Schaeffer (1926) in the salt water tank of the laboratory at Tortugas.

22. *Flamella magnifica* Schaeffer, 1926.

Schaeffer (1926) discovered this amoeba among blue-green algae in cultures from Key West and Tortugas.

23. *Cachliopodium gulosum* Schaeffer, 1926.

In his description of the species Schaeffer (1926) gave the localities (p. 106) as Cold Spring Harbor and Great South Bay, Long Island, where the organism was found on eelgrass and other seaweed. His table (p. 22) indicates that it was also observed at Tortugas.

Order 4 TESTACEA Schultze 1854

Most of the Testacea are fresh-water forms. The writer knows of none reported from the Gulf of Mexico.

Order 5 FORAMINIFERA D'Orbigny 1826

This large group, with many representatives in the Gulf of Mexico, is treated separately.[4]

Subclass 2 *Actinopoda* Calkins 1909

Order 1 HELIOZOA Haeckel 1866

Most of these organisms are inhabitants of fresh water. The writer does not know of any which have been reported from the Gulf of Mexico.

Order 2 RADIOLARIA J. Müller 1858

The Radiolaria, a very large order, are exclusively marine and are widely distributed in the warmer waters of the seas. Although they may occur in the Gulf of Mexico, the writer is not familiar with studies on them there.

Class 3 SPOROZOA Leukart 1879

Our knowledge of the Sporozoa of the Gulf of Mexico is practically limited to the information which has grown out of investigations into causes of oyster mortality, especially those recently conducted by the Texas Agricultural and Mechanical Research Foundation along the coasts of Louisiana, Texas, and Mississippi. Although the Sporozoa studied in investigations were primarily those parasitic in oysters, several were observed, also, in various decapod Crustacea, and very limited observations were made on forms in annelids. Sporozoa are common parasites in essentially all the major groups of animals, and the few studies on forms from the Gulf give promise that intensive search for members of this neglected group would reveal a great wealth of new and known species there. With one or two exceptions, which are considered below, nothing is known about the general distribution of most species.

Subclass 1 *Telosporidia* Schaudinn 1900

Order 1 GREGARINIDA Lankester 1866

Suborder 1 EUGREGARINARIA Dofle in 1901

Tribe 1 *Haplocyta* Lankester 1885

Family MONOCYSTIDAE Stein

1. An "acephaline gregarine" Wichterman, 1942.

Host: *Pontodrilus bermudensis* Beddard, a littoral oligochaete.

Organs involved: Intestine and seminal vesicles.

Locality: Observed at Loggerhead Key, Tortugas.

Remarks: Wichterman's (1942) figures 18–20 suggest that this gregarine may be one of the Monocystidae. Hence, it is placed provisionally in this family.

Tribe 2 *Septata* Lankester 1885

Family POROSPORIDAE Labbé

2. *Nematopsis ostrearum* Prytherch, 1938 (partim) Sprague, 1949.

Hosts: Molluscan host the oyster *Crassostrea virginica* (Gmelin); decapodan hosts the mud crabs *Panopeus herbstii* Milne Edwards, *Eurypanopeus depressus* (Smith) and *Eurytium limosum* (Say).

Organs involved: The intestinal tract of the crab and almost all the organs (especially mantle) of the oyster. The gamontocysts attached to the rectum of the crab occur only in the extreme posterior portion of the organ.

Widely distributed along the Gulf and Atlantic coasts. Landau and Galtsoff (1951) found *Nema-*

[4] See article by F. B. Phleger and F. L. Parker, pp. 235–241 of this book.

topsis spores, probably this species, in Delaware Bay and as far north as Great South Bay, New York.

The northern limit of the known range is based on Prytherch's (1938, 1940) observation of *Nematopsis* spores in oysters as far north as Mobjack Bay, Virginia.[5] Although *N. ostrearum*, as originally described, contained two species, it is believed that only the one considered at this time extends as far north as Virginia. (See *N. prytherchi* below.)

3. *Nematopsis prytherchi* Sprague, 1949.

Hosts: Molluscan host the oyster *Crassostrea virginica* (Gmelin), decapodan host the stone crab *Menippe mercenaria* (Say).

Organs involved: The intestinal tract of the crab and the gills (principally) of the oyster. The gamontocysts are distributed along the entire rectum of the crab.

Distribution: Widely distributed along the Gulf coast and probably to North Carolina on the Atlantic coast. North Carolina is presumed to be the northern limit of the range of this species since its only known decapodan host, according to Rathbun (1930), occurs only that far north.

Remarks: This species was separated from *Nematopsis ostrearum* Prytherch, 1938, in a preliminary note by Sprague in 1949 and described in detail later (1950), with an account of extensive infection experiments, in an unpublished report submitted to Texas Agricultural and Mechanical Research Foundation.

4. *Nematopsis penaeus* n. sp.=*Nematopsis* (?) sp. Sprague, 1950.

Hosts: *Penaeus aztecus* Ives, one of the common commercial shrimp, is here designated as the host, although the parasite seems to be identical with one in *P. setiferus* (Linn.). No intermediate host is known. The oyster, *Crassostrea virginica* (Gmelin), has been eliminated, by means of infection experiments, as a possible host.

Organs involved: Intestinal tract of the decapod.

Vegetative stages: Similar to those of well-known species of *Nematopsis*. Early stages are small spherical bodies intracellular in the intestinal epithelium. Epimerite spherical. Young gregarines early become associated in chains of two or more individuals in linear or bifurcated syzygy. The posterior extremity in older associations often appears somewhat more truncate than in the described species of *Nematopsis*.

Gamontocysts: Spherical; 132–260 microns in diameter, the mean diameter being 177 microns (based on measurements of 35 cysts from 2 host specimens); attached to the chitinous lining of the rectum and distributed along its entire length. Note: "Gamontocyst" is used here in accordance with the new terminology recently proposed by Filipponi (1949).

Gymnospores: Smooth, spherical aggregates of cells when mature. They are among the largest known, being comparable in size with only those of *N. prytherchi*. (Unfortunately, measurements on living gymnospores are not on hand, and measurements of stained ones are of little value for comparing with living gymnospores of other species.)

Distribution: Barataria Bay, Louisiana, is here designated as the type locality. The organism, however, is probably widely distributed along the Gulf and Atlantic coasts, since it has been found in every one of hundreds of shrimp examined from the Louisiana coast when the examination was made soon after the shrimp were collected.

Comparison and affinities: The vegetative stages are similar to those of known species of *Nematopsis*. Gymnospores are very large, only those of *N. prytherchi* being comparable in size. Gamontocysts are about the same size as those of *N. maraisi* (Léger and Duboscq, 1911) in the crab *Portunus depurator* and are exceeded in size only by those of *Porospora gigantea* (Van Beneden 1869); in being distributed along the entire rectum of the host they are like *P. gigantea* in the European lobster and different from any known species of *Nematopsis* excepting *N. pyrtherchi* in the stone crab. To summarize, *N. penaeus* resembles *N. maraisi* in size of gamontocyst but is distinctly different in having a larger gymnospore; it resembles *N. prytherchi* in size of gymnospore and distribution of gamontocyst but has a larger gamontocyst and different host specificity; it resembles *Porospora gigantea* also in distribution of the gamontocysts in the rectum of the host and by being an inhabitant of one of the macroura but has a distinctly larger gymnospore and is strikingly different in the vegetative stages.

The writer's attention was first called to this gregarine, the third member of the Porosporidae

[5] Reported also from Delaware Bay and Great South Bay, New York, by H. Landau and P. S. Galtsoff (1951, Texas Jour. Sci., vol. 3).

described from American waters, by Prytherch (personal communication, 1946). Although the known stages of the parasite are indistinguishable from corresponding stages of *Nematopsis* (some of them different from corresponding stages of Porospora, the only other genus which it resembles), it cannot be assigned to *Nematopsis* with confidence until its life history is completely known. Since it has gymnospores it can be placed in Porosporidae (members of which are unique among gregarines in having gymnospores and alternation of hosts), but there is not the slightest clue as to what the intermediate host (if any) may be. Since generic characters of the two genera now in the family are based upon stages in the intermediate host, definite generic determination cannot now be made.

Sprague (1950) concluded, primarily on the basis of infection experiments, that the oyster is not the intermediate host of this gregarine. If *Nematopsis penaeus* has an intermediate host one would expect the latter to be an organism (possibly a small mollusk or a worm) which constitutes the chief or a very prominent item in the diet of shrimp. The last statement is based upon the belief that the host must acquire a new infestation almost every day in order to maintain, at all times, a large gregarine population consisting of individuals representing essentially every stage of development. The problem of discovering the possible intermediate host is complicated by the remarkable fact that, as Burkenroad has pointed out in a personal communication, we are almost completely ignorant of the feeding habits of the very familiar decapodan host. The possibility that the shrimp become directly reinfested by ingesting the gymnospores which pass from their intestines requires further consideration, although experimental data by Sprague (1950) suggest that such studies would give negative results. Shrimp maintained in the laboratory and fed upon oysters (containing *Nematopsis* spores) and fish became entirely free of gregarines in less than a week. The tentative conclusion from those data is that the shrimp neither reinfest themselves nor become infested by eating oysters (although *Nematopsis* spores from oysters readily germinate in shrimp), but that they acquire the gregarines by feeding almost daily upon some specific but unknown organism common in their natural habitat.

Since these gregarines are intracellular in the intestinal epithelium of the host during their early development, and since the host seems to acquire great numbers of them almost daily, the intestinal epithelium is subject to appreciable damage by the parasites. In view of the great economic importance of shrimp, the host-parasite relation of these two organisms is of more than academic interest and deserves intensive investigation.

5. "Gregarine cysts" were reported by Pearse (1932a) in the calico crab, *Eriphia gonagra* (Fabricus) in Tortugas.

Although Pearse (1932a) merely mentioned gregarine cysts seen on the walls of the rectum of the crab, it is quite probable that they were *Nematopsis*. Not only are *Nematopsis* cysts attached to the rectum in many species of crabs very common, but *N. legeri* (de Beauchamp, 1910), one of the best known species, occurs in a species of Eriphia, *E. spinifrons* Herbst, on the coast of France.

UNIDENTIFIED SPECIES OF *NEMATOPSIS*

As in Europe, several species of mollusks in American waters have been found to harbor *Nematopsis* spores of undetermined species. Although some of those spores may represent stages of well-known species of *Nematopsis*, it is quite probable that others represent undescribed species. A list of those mollusks is given in the table below.

TABLE 1.—*American mollusks in which spores of undetermined species of* Nematopsis *have been observed*

Host species	Organs involved	Locality	Author
From Gulf of Mexico:			
Ostrea cristata	(?)	Port Aransas, Tex.	S. H. Hopkins (unpublished).
Modiolus demissus	Mantle and gill.	Grand Isle, La.	Sprague (unpublished).
Mytilus recurvus	(?)	Barataria Bay, La.	Do.
Ensis minor	Mantle	do	Do.
From southern waters, possibly including the Gulf of Mexico:			
Pecten gibbosus	(?)	(?)	Prytherch (1940).
Anomia simplex	(?)	(?)	Do.
Ostrea equestris [6]	(?)	(?)	Do.
Modiolus demissus	(?)	(?)	Do.
Venus ziczac	(?)	(?)	Do
Martesia cuneiformis	(?)	(?)	Do.
Urosalpinx cinerea	(?)	(?)	Do.
From Pacific Coast:			
Ostrea chilensis	(?)	Gulf of Panama.	Landau and Galtsoff, 1951.

[6] Hopkins, S. H., has called attention to the fact that this should be *O. cristata* since *O. equestris* occurs not in North America but in South America.

Unidentified gregarines were found in Barataria Bay, Louisiana, by Hopkins (personal communi-

cation, 1950) in a common tube-dwelling annelid, *Spirochaetopterus* sp., and in the intestines of *Polydora websteri* (Hartman), a common polychaete infesting the shells of oysters.

Order 2 COCCIDIA Leuckart 1879

The writer knows of no members of this order which have been reported from the Gulf of Mexico. It is possible, however, that they may be present in some of the numerous species of vertebrates there.

Order 3 HAEMOSPORIDIA Danilewsky 1886

Excepting Plasmodium, which occurs in the vicinity of the Gulf but which does not seem to fall within the scope of this paper, the author knows of no Haemosporidia reported from the area.

Subclass 2 *Acnidosporidia* Cépède 1911

Order 1 SARCOSPORIDIA Balbiani 1882

The Sarcosporidia, being chiefly parasitic in the muscle tissues of mammals, seem not to have been reported from the Gulf.

Order 2 HAPLOSPORIDIA Caullery and Mesnil 1899

It is customary to place in this order any organism which seems to have sporozoan affinities but does not belong to any other order. Consequently, Haplosporidia includes a heterogeneous assemblage of unrelated organisms. Some of them should probably be assigned to new orders, and some others may be more closely related to fungi than to Sporozoa. The one common characteristic is the lack of polar filaments in the spores. Although there are many types of spores represented in this order, some of them have a striking superficial resemblance to those of Microsporidia. Only one species (previously unrecorded) which can unquestionably be properly assigned to Haplosporidia seems to be known from the Gulf. Two others are provisionally included here pending further information.

1. *Haplosporidium* sp.

Observed by Sprague in January 1948 in the vicinity of Grand Isle, Louisiana, in only one of many specimens of the common mud crab, *Panopeus herbstii* Milne Edwards (kindly identified by F. A. Chace, Jr., of the United States National Museum).

The intestine, covered on the outside with the spores, has a conspicuous dark brown appearance.

2. "A haplosporidian (microsporidian?)".
In *Gymnophallus* sp. (metacercariae).

A trematode parasite of the clam *Donax* sp. from Port Aransas, Texas, was reported by Hopkins (1950) in a personal communication to the author.

3. *Dermocystidium marinum* Mackin, Owen and Collier, 1950.

Found to be widely distributed in *Crassostrea virginica* (Gmelin), the commercial oyster, along the Gulf coast. It infects any of the host tissues, especially the intestinal epithelium, adductor muscle, gills, mantle, and heart. Although there is great uncertainty about the taxonomic position of the genus *Dermocystidium*, it is usually placed in the Haplosporidia (see footnote, p. 244). According to Mackin et al. (1950), the parasite has been found associated "with dead or dying oysters under certain environmental conditions, the limits of which can be reasonably well-defined. The chief controlling factors appear to be temperature and salinity, low temperature and low salinity evidently retarding the development of the infestation" (p. 329).

Subclass 2 *Cnidosporidia* Doflein 1901

Order 1 MYXOSPORIDIA Bütschli 1881

The writer knows of no Myxosporidia which have been reported from the Gulf of Mexico, although there is no reason to doubt that they occur there. As Kudo (1946) has pointed out, these organisms are exclusively parasites of lower vertebrates, especially fish. Davis (1917) and others have described numerous species found in various fish of the Atlantic coast. The fact that many of the same species of fish occur also in the Gulf of Mexico is reason to suspect that many of the known Myxosporidia also occur there. Doubtless, a search for these neglected forms would be rewarded by the discovery of many new and known species.

Order 2 ACTINOMYXIDIA Stolç 1899

This order contains but few known species, all occurring in fresh or salt-water annelids, and none apparently having been reported from the Gulf. In view of the great variety and numbers of annelids in the Gulf, however, it is quite possible that species of Actinomyxidia occur there.

Order 3 MICROSPORIDIA Balbiani 1883

The Microsporidia, being typically parasites of arthropods and fish (although they are represented in several animal phyla), are probably common parasites in animals of the Gulf. The

Crustacea, in particular, are very susceptible hosts and are abundantly represented in the Gulf. Nevertheless, Microsporidia occurring in the Gulf, even in economically very important animals, seem to have been almost completely neglected. The writer knows of only three species which have been definitely identified as Microsporidia, although others have probably been observed in the Gulf.

Family NOSEMATIDAE Labbé

1. *Nosema nelsoni* Sprague, 1950.

In the muscles of *Penaeus aztecus* Ives, one of the common commercial shrimp, was reported from Barataria Bay, Louisiana, but apparently is widely distributed along the Gulf and Atlantic coasts.

Burkenroad (personal communication) believes that he has seen the parasite also in *P. setiferus* (Linn.). It is remarkable that this very common parasite which causes a conspicuous discoloration of the host and an appreciable economic loss to the shrimp industry seems never to have been the subject of serious investigation.

2. *Thelohania penaei* Sprague, 1950.

In sex organs of *Penaeus setiferus* (Linn.), a common commercial shrimp, was reported from the vicinity of Grand Isle, Louisiana, but probably is widely distributed.

After Sprague (1950a) described the polar filament of this parasite as being unique in its structure he learned that Jírovec (1937) described a very similar polar filament in a new species of *Plistophora*, *P. schafernai*, which he found in *Daphnia pulex*. The author is pleased to take this opportunity to correct his error.

Burkenroad (personal communication) thinks he has seen this parasite also in *Penaeus aztecus* Ives.

Since species of *Thelohania* in the sex organs of certain other decapods allegedly cause parasitic castration, the possible role of *T. penaei* in the fluctuation of shrimp populations is a matter of considerable economic interest and should be thoroughly investigated. In this connection, Viosca (1943) has made some interesting observations. He stated (p. 276), "Some years ago (1919) about 90 percent of the salt water shrimp, *Penaeus setiferus*, existing in the waters along the Louisiana coast were infected with a protozoan disease which destroyed their reproductive organs. Yet during the following two years, 1920 and 1921, the shrimp crops were the largest then known and were greater than for several succeeding years. Thus, 10 percent of the adult shrimp population produced a larger succeeding crop than 10 times their number did the preceding year, while the large 1921 crop again produced a smaller number. This evidence shows that with a prolific species, the food supply and other ecological factors are far more important than the actual number of eggs laid."

3. *Thelohania* sp. Sprague, 1950.

In all the muscles of *Petrolisthes armatus* (Gibbes), a small flat crab very common on oyster reefs. Known only from a particular shell reef near Grand Terre Island in Barataria Bay, Louisiana.

Pending further information on the affinities of this parasite, it was not named at the time it was reported. It is now definitely believed to be distinct from previously recorded species.

Order 4 HELICOSPORIDIA Kudo 1931

This order contains only one species, and there is no reason to suspect that any occurs in the Gulf of Mexico.

Subphylum 2 CILIOPHORA Doflein 1901

Class 1 CILIATA Perty 1852

Subclass 1 *Protociliata* Metcalf 1918

Most of the Protociliata inhabit the colon of Salientia, rarely marine fish or other vertebrates. Probably none has been observed in vertebrates of the Gulf of Mexico.

Subclass 2 *Euciliata* Metcalf 1918

Although more than half of the ciliates reported from the Gulf of Mexico have been new species, there is no doubt that numerous previously known ones are represented there. Since the free-living ciliates are essentially cosmopolitan, it is not surprising when one finds a particular form in any locality where there is a favorable habitat. Bullington (1940), and undoubtedly many other persons as well, saw many ciliates which he did not have an opportunity to identify.

Order 1 HOLOTRICHA Stein 1859

Suborder 1 ASTOMATA Schwiakoff 1896

Family ANOPLOPHRYIDAE Cépède

1. *Anoplophrya macronucleata* Wichterman, 1942.

In the intestine of *Pontodrilus bermudensis* Beddard, a littoral oligochaete. Discovered by Wichterman (1942) in the vicinity of Loggerhead Key, Tortugas.

2. "A ciliate resembling Rhizocaryum."

Was found by S. H. Hopkins (personal communication, 1950) in the intestines of *Polydora websteri* (Hartman). Very common in Barataria Bay, Louisiana.

Family INTOSHELLINIDAE Cépède

3. *Maupasella leptas* Wichterman, 1942.

In the intestine of *Pontodrilus bermudensis* Beddard, a littoral oligochaete. Discovered by Wichterman (1942) in the vicinity of Loggerhead Key, Tortugas.

Suborder 2 GYMNOSTOMATA Bütschli 1889

Tribe 1 *Prostomata* Schewiakoff

Family SPATHIDIIDAE Kahl

4. *Paraspathidium trichostomum* Noland, 1937

Noland (1937) found a few individuals of this species near Englewood, Florida, and created a new genus to contain the species.

Family DIDINIIDAE Poche

5. *Mesodinium pulex* (Claparède and Lachman, 1858).

Noland (1937) found this species frequently in marine cultures at Bass Biological Laboratory, Englewood, Florida.

6. *Mesodinium acarus* Stein, 1862.

Observed in cultures at Bass Biological Laboratory, Englewood, Florida, by Noland (1937) who stated that he was familiar with the same species in fresh water.

Family COLEPIDAE Claparède and Lachmann

7. *Coleps spiralis* Noland, 1937.

Noland (1937) discovered this ciliate at Bass Biological Laboratory, Englewood, Florida.

8. *Coleps tesselatus* Kahl, 1930.

Noland (1937) observed this ciliate in the vicinity of Englewood, Florida.

9. *Coleps heteracanthus* Noland, 1937.

Discovered by Noland (1937) in the vicinity of Englewood, Florida.

10. *Coleps pulcher* Kahl.

Observed by Noland (1937) in a salt spring near Englewood, Florida.

11. *Coleps* sp. Bullington, 1931.

Bullington (1931) observed two undetermined species of *Coleps* at Tortugas.

Family HOLOPHRYIDAE Schouteden

12. *Plagiocampa marina* Kahl.

Reported by Noland (1937) from the vicinity of Englewood, Florida.

13. *Placus socialis* (Fabre-Domergue, 1889).

Reported by Noland (1937) from the vicinity of Englewood, Florida.

14. *Trachelocera dracontoides* Bullington, 1940.

Discovered by Bullington (1940) in 1930, exact locality unrecorded, and in 1939 in cultures from moat at Fort Jefferson, Garden Key, Tortugas.

15. *Trachelocera subviridis* Sauerbrey, 1928.

Observed by Noland (1937) in a salt spring near Englewood, Florida.

16. *Trachelocera* sp.

Observed by Pearse (1932) in Pond 1 on Long Key, Tortugas.

Tribe 2 *Pleurostomata* Schewiakoff

Family AMPHILEPTIDAE Schouteden

17. *Kentrophorus fasciolatum* Sauerbrey, 1928.

Noland (1937) observed this ciliate in sediment over a sandy bottom in sea water near Englewood, Florida.

Tribe 3 *Hypostomata* Schewiakoff

Family NASSULIDAE Schouteden

18. *Nassula gigantea* Bullington, 1940.

Found by Bullington (1940) several times on algae in the bottom of the moat on the south side of Fort Jefferson, Garden Key, Tortugas.

19. *Paranassula microstoma* (Claparède and Lachmann, 1858).

Noland (1937, p. 166) found several specimens in "a shallow marine estuary just inside the beach ridge from the Gulf of Mexico, and connected indirectly through a pass with the Gulf."

Suborder 3 TRICHOSTOMATA Bütschli 1889

Family ENTORHIPIDIIDAE Madsen

20. *Entodiscus sabulonis* Powers, 1935.

Found by Powers (1935) in the intestines of sea urchins, *Clypeaster rosaceus* and *C. subdepressus*, in shallow water at Tortugas.

21. "Form L" Powers, 1935.

Powers (1935) considered this unidentified ciliate infesting *Clypeaster subdepressus* in Tortugas to be either a variety of *E. sabulonis* or a closely related species.

22. *Biggaria bermudensis* (Biggar, 1932).

According to Powers (1933, p. 279), "While this species may be found in any echinoid host, it seems to prefer *Lytechinus variegatus* or *Tripneustes esculentus*," infesting their intestines. The species is considered by Powers (1933, 1935) as identical with form "D" which Jacobs (1911) discovered at Tortugas and indicated that it has been observed also at Bermuda and Beaufort, North Carolina.

23. *Anophrys elongata* Biggar, 1932.

According to Powers (1935) this ciliate is identical with form "C" of Jacobs (1911). It was found at Bermuda and Tortugas in all the species of sea urchins examined. Biggar

(1932) found it in *Lytechinus variegatus* and *Echinometrus lacunter*.

24. *Anophrys aglycus* Powers, 1935.

Powers (1935) found this ciliate present in the intestines of all species of sea urchins living near the tide line in Tortugas though not abundant in any of them. *Tripneustes esculentus* collected near the reef was the best example of infestation with this form.

25. "Form M" Powers, 1935.

In the intestines of the sea urchins *Trypneustes esculentus* and *Lytechinus variegatus* in Tortugas. Powers (1935) noted that this form was similar both to *Cohnilembus caeci* Powers, 1935 (see below), and *Anophrys vermiformis* Powers, 1933, the latter common to *Lytechinus variegatus* at Beaufort, North Carolina. It is listed provisionally here with the Entorhipidiidae simply for the sake of convenience; there is no implication that the writer holds an opinion as to its taxonomic position.

Suborder 4 HYMENOSTOMATA Hickson 1903

Family FRONTONIIDAE Kahl

26. *Frontonia schaefferi* Bullington, 1939.

Discovered by Bullington (1939a, 1940) in a pool at East Key, Tortugas.

27. *Frontonia ocularis* Bullington, 1939.

In Tortugas.

28. *Uronema marina* Dujardin.

Observed by Pearse (1932) in Pool 5 on Garden Key, Tortugas.

29. *Uronema pleuricaudatum* Noland, 1937.

Discovered by Noland (1937) in cultures at Bass Biological Laboratory, Englewood, Florida.

Family OPHRYOGLENIDAE Kent

30. *Ophryoglena frontania* Bullington, 1940.

Found by Bullington (1930) in a pool on East Key and later (1939) in cultures from the moat around Fort Jefferson on Garden Key, Tortugas.

31. *Pleuronema setigerum* Calkins, 1902.

Originally discovered at Woods Hole, Massachusetts, this species was found by Noland (1937) in the vicinity of Englewood, Florida.

32. *Pleuronema coronatum* Kent.

Observed by Noland (1937) in the vicinity of Englewood, Florida.

33. *Pleuronema marinum* Dujardin, 1841.

Observed by Noland (1937) in the vicinity of Englewood, Florida.

34. *Cyclidium rhabdotectum* Powers, 1935.

In Tortugas found in the sea urchins *Centrechinus antillarum*, *Echinometra lucunter*, *Tripneustes esculentus* and *Clypeaster rosaceus*, being rare in the last host species. Powers (1935) considered it quite likely that this species is the one which Jacobs (1912) designated as form "A."

35. *Histobalantidium semisetatum* Noland, 1937.

Discovered by Noland (1937) in the vicinity of Englewood, Florida.

Family COHNILEMBIDAE Kahl

36. *Cohnilembus caeci* Powers, 1935.

Powers (1935) who discovered the species at Tortugas remarked that *C. caeci*, commonly found in any of the littoral echinoids, has a marked predilection for *Tripneustes esculentus*.

Suborder 5 THIGMOTRICHA Chatton and Lwoff 1926

Family HYSTEROCINETIDAE Diesing

37. *Hysterocineta pontodrilus* Wichterman, 1942.

In intestines of *Pontodrilus bermudensis* Beddard, a littoral oligochaete in the vicinity of Loggerhead Key, Tortugas (Wichterman 1942).

Order 2 SPIROTRICHA Bütschli 1889

Suborder 1 HETEROTRICHA Stein 1859

Family METOPIDAE Kahl

1. *Metopus brevicristatus* Powers, 1935.

Limited to the intestines of the sea urchin *Clypeaster rosaceus* in Tortugas. This ciliate seems to be the one designated by Powers (1933) in a preliminary note as form "G."

2. *Metopus histophagus* Powers, 1935.

Observed only in intestines of the sea urchin, *Clypeaster subdepressus*, in Tortugas.

3. *Metopus rotundus* Lucas, 1934.

Known only from the intestines of the sea urchin, *Centrechinus antillarum*. Originally described from Bermuda, this ciliate was reported from Tortugas by Powers (1935).

According to Powers (1935, p. 302), "Lucas (1934) reports this form as the sole infestant of three specimens of *Centrechinus antillarum* from Bermuda. At Tortugas, *M. rotundas* was always found in company with other ciliates." In a preliminary note by Powers (1933) this ciliate apparently was designated as form "J."

4. *Metopus circumlabens* Biggar, 1932.

This species has been found in the intestines of various sea urchins in Bermuda and Tortugas. Observed in *Centrechinus antillarum* and *Echinometra lucunter* by Jacobs (1912), Biggar (1932), Lucas (1934), and Powers (1935); in *Lytechinus variegatus* by both Jacobs and Powers; in *Tripneustes esculentus* by Powers (1935); rarely in *Clypeaster rosaceus* and *C. subdepressus* by Powers.

Family SPIROSTOMIDAE Kent

5. *Gruberia lanceolatum* (Gruber 1884).

This free-living ciliate is widely distributed, having been observed by Bullington (1940) not only at Tortugas but also at Cold Spring Harbor, Long Island, and Beaufort, North Carolina.

6. "A form related to *Gruberia calkinsi*" was observed by Anigstein (personal communication 1950) on the northeast shore of Galveston Island in Galveston Channel, Texas.

Family CONDYLOSTOMIDAE Kahl

7. *Condylostoma granulosum* Bullington, 1940.

Bullington (1940) found this ciliate in pools on Bush Key, Tortugas, and in brackish water ponds at Cold Spring Harbor.

8. *Condylostoma minutum* Bullington, 1940.

Discovered by Bullington (1940) at Tortugas, exact locality unrecorded.

9. *Condylostoma magnum* Spiegel, 1926.

Observed by Bullington (1940) in pools on Bush Key Reef, Tortugas, at extreme low tide.

10. Unidentified species of *Condylostoma*.

This species was observed by Pearse (1932) in Pond 1 on Long Key, Tortugas.

Family STENTORIDAE Carus

11. *Stentor auriculatus* Kahl, 1932.

Found by Bullington (1940) in old cultures in the laboratory at Tortugas.

12. Unidentified species of *Stentor*.

Observed by Pearse (1932) in Pond 1 on Long Key, Tortugas.

Family FOLLICULINIDAE Dons

13. A ciliate resembling *Folliculina moebiusi* Kahl.

This specimen was called to the attention of the writer in the summer of 1938 by J. H. Roberts of Louisiana State University. The organism was in a sample of sediment from the bottom of Barataria Bay, Louisiana.

Family PERITROMIDAE Stein

14. *Peritromus tortugensis* Bullington, 1940.

Discovered by Bullington (1940, p. 195) "in algal cultures from near the tip of Long Key at very low tide," Tortugas.

Suborder 2 OLIGOTRICHA Bütschli 1887

Family HALTERIIDAE Claparéde and Lachmann

15. *Halteria*.

Pearse (1932) observed an unidentified species in Pond 1 on Long Key, Tortugas.

16. *Strombidium alveolare* Bullington, 1940.

Discovered by Bullington (1940) in floating material at the dock at Fort Jefferson, Garden Key, Tortugas.

Suborder 4 HYPOTRICHA Stein 1859

Family OXYTRICHIDAE Kent

17. *Oxytricha*.

Bullington (1935) mentioned having observed *Oxytricha* at Tortugas.

18. *Holosticha rubra* (Ehrenberg 1838).

Found by Bullington (1940) at various localities at Tortugas and at Beaufort, North Carolina.

19. *Epiclintes caudatus* Bullington, 1940.

Discovered by Bullington (1940), exact locality unrecorded, at Tortugas.

20. *Stylonychia* sp. Anigstein, 1950.

Anigstein (personal communication 1950) observed an unidentified species of *Stylonychia* on the northeast shore of Galveston Island in Galveston Channel, Texas.

21. Stylonichia.

Pearse (1932) observed an unidentified species of *Stylonychia* in Pond 2 on Long Key, Tortugas.

22. Strongylidium.

Pearse (1932) observed an unidentified species of *Strongylidium* in Pond 2 on Long Key, Tortugas.

23. *Uncinata gigantea* Bullington, 1940.

Bullington (1940) discovered this ciliate, for which he created a new genus, at Tortugas. He believed it came from Long Key but was not certain. Although Bullington did not assign the new genus to a family, it apparently belongs to the Oxytrichidae.

24. Unidentified sp.

Anigstein (1949) made physiological studies on an undetermined member of the Oxytrichidae collected along the northeast shore of Galveston Island, Texas.

Family EUPLOTIDAE Claus

25. *Euplotes charon* (Müller).

Observed by Anigstein (personal communication 1950) along the northeast shore of Galveston Island in Galveston Channel, Texas.

26. *Euplotidium agitatum* Noland, 1937.

Discovered by Noland (1937) in two samples from Lemon Bay near Bass Biological Laboratory and (p. 170) "in squeezings from half-dead sponges brought up by sponge fishermen from about 25 feet of water 10 miles out in the Gulf of Mexico off Tarpon Springs, Florida." Noland created a new genus to contain the species.

27. *Uronychia heinrothi* Buddenbrock, 1920.

Observed by Bullington (1940) in various localities at Tortugas.

Family PARAEUPLOTIDAE Wichterman

28. *Paraeuplotes tortugensis* Wichterman, 1942.

Wichterman (1940, 1942) found this ciliate, for which he created a new family and a new genus, in abundance on the coral, *Eunicea crassa*, at Tortugas.

FAMILY UNKNOWN

29. Unidentified sp.

Pearse (1932) observed unidentified hypotrichous infusorians in Pond 1 on Long Key and Pool 5 on Garden Key, Tortugas.

30. *Gastrocirrhus stentoreus* Bullington, 1940.

Discovered by Bullington from an unrecorded locality believed to have been Long Key, Tortugas.

Bullington (1940) stated that this species is similar to *G. intermedius* Lepsi, 1928, for which the genus was

created, in having characters of both heterotrichs and hypotrichs. He further stated that Kahl (1935) was unable to classify Lepsi's species.

Order 3 CHONOTRICHA Wallengren 1895

The writer does not know of any member of this order which has been reported from the Gulf of Mexico.

Order 4 PERITRICHA Stein 1859

Suborder 1 SESSALIA Kahl 1935

Tribe 1 *Aloricata* Kahl

Family EPISTYLIDAE Kent

1. *Epistylis.*

Pearse (1932a) found undetermined species of *Epistylis* on the gills of the following crabs at Tortugas: *Coenobita clypeastus* (Herbst) from Garden Key and Long Key, *Geograpsus lividus* (Milne Edwards) from Bird Key Reef, and *Pachygrapsus transversus* (Gibbes) from Long Key. He also found *Epistylis* on the abdominal appendages of the isopod, *Ligyda exotica* (Roux) from the walls of the moat at Fort Jefferson on Garden Key.

Family VORTICELLIDAE Fromental

2. *Vorticella marina* Greeff, 1870.

Observed by Pearse (1932) in Pond 2 on Long Key, Tortugas. Noland and Finley (1931, p. 97) held the opinion that "*V. marina* Greeff, 1870, is possibly identical with *V. nebulifera* O. F. M., which was originally described from salt water. Further study of the marine Vorticellae is necessary before synonymy of the marine species can be definitely settled."

Class SUCTORIA Claparède and Lachmann 1858

Although it is probable that members of this group are common in the Gulf of Mexico, the writer is not familiar with reports of their occurrence there.

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CHAPTER VIII
SPONGES, COELENTERATES, AND CTENOPHORES

THE PORIFERA OF THE GULF OF MEXICO [1]

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Sponges are one of the dominant sessile invertebrate groups in the Gulf of Mexico: they extend from the intertidal zone down to the deepest parts of the basin, and almost all of the firm or rocky sections of the bottom provide attachment for them.

Members of the class Hyalospongea (Hexactinellidea) are, almost without exception, limited to the deeper waters of the Gulf beyond the 100-fathom curve. These sponges possess siliceous spicules in which (typically) six rays radiate from a central point; frequently, the spicules are fused together forming a basket-like skeleton. Spongin is never present in this group.

In contrast to the Hyalospongea, representatives of the class Calcispongea are seldom, if ever, found in deep water. These sponges, unique in having spicules of calcareous material, are usually restricted to shallow water. They are not conspicuous; typically, they are encrusting forms or tubiform in shape but only a few centimeters in height.

The major sponge group in the Gulf of Mexico, both from number of genera and from the range of distribution, is the class Demospongea. Possessing more or less spongin, and when spicules are present having unfused spicules of siliceous material, these sponges occur throughout the Gulf extending from the shallow coastal waters down to the deepest off-shore sections of the basin.

The sponge bars or reefs of the eastern Gulf are quite typical of the habitat and ecology of the sponges in shallow to moderate depths. These so-called reefs are sections of rocky outcroppings that are elevated a few inches to a few feet above the general bottom profile. They are more or less densely covered with commercial and non-commercial sponges, coral (usually *Oculina*), and Alcyonaria. The other bottom-dwelling marine groups (such as mollusks, annelids, Crustacea, ascidians) are associated with the dominant groups. The floor of the Gulf between the bars is sparsely populated. The majority of the animals and plants are concentrated on the rocky ledges and outcroppings.

The most abundant sponges on these reefs are of several genera representing most of the orders of the class Demospongea. Several species of *Ircinia* are quite common as are *Verongia*, *Spheciospongia*, and several Axinellid and Ancorinid sponges; *Cliona* is very abundant, boring into molluscan shells, coral, and the rock itself. The sponge population is rich both in variety and in number of individuals; for this reason no attempt is made to discuss it in taxonomic detail in this résumé.

Some of the sponges of the Gulf are of world-wide distribution, i. e., *Dysidea fragilis*, while others are typically West Indian, and a few are probably restricted to the Gulf. The West Indian sponge fauna may be a single regional population with only minor locational differences. Water currents of the Caribbean, the Gulf, and the southern portion of the western Atlantic off Florida and the Bahama Islands have been shown to to carry a sponge disease from one point to many others in this region; it is therefore permissible to suggest that the same currents would be equally effective in distributing sponge larvae.

The commercial sponges of Florida, the Bahamas, Cuba, and British Honduras are all quite similar: the sheepswool sponge, *Hippiospongia lachne*, is the most valuable sponge now available for the market. Reef, glove, yellow, and grass sponges, all members of the genus *Spongia*, are of less value and are therefore less eagerly sought by the sponge fishermen.

Two methods, in general, are used in the West Indian region for the collection of commercial sponges. Hooking is practiced in waters of less than 7 or 8 fathoms throughout the entire zone, and light-weight, full diving rigs are used in the Gulf of Mexico in depths of less than 20 fathoms.

[1] Contribution No. 105, Marine Laboratory, University of Miami.

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In addition to these two major methods a few native islander fishermen skin-dive for sponges in shallow water, and a few Florida sponge fishermen have begun in the past few years to drag tines and other types of dredges in order to obtain more sponges with less work.

As a result of the constantly decreasing supply of natural sponges there have been repeated attempts in the past half century to establish sponge farms in the shallow coastal waters of Florida and the other Caribbean sponge producing areas. Practical as they now are from a biological point of view, these farms have always failed because of economic difficulties. It is now entirely possible, however, to produce artificially propagated sponges as a sound commercial venture.

In addition to the biological studies on the distribution and growth of the Gulf of Mexico porifera, there have been biochemical studies carried out on the lipids, the carbohydrates, and the general chemical constitution of several of the more common marine sponges of this region.

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BIOLOGY OF THE COMMERCIAL SPONGES[1]

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All commercial sponges of the Gulf of Mexico belong to the family Spongiidae. They are characterized by a lack of spicules and by the presence of a skeleton consisting of a network of anastomosing spongin fibers. The canal system is of the leucon type. Subdermal cavities which act as vestibules to either the incurrent or excurrent canal systems, or both, are present to a varying degree and are particularly noticeable in the velvet sponge, *Hippiospongia gossypina*.

The external form is roughly subspherical in the case of sheepswool sponge, *Hippiospongia lachne*, the yellow sponge, *Spongia zimocca* ss. *barbara*, hard head, *Spongia officinalis* ss. *dura*, and the velvet sponge. The grass sponge, *Spongia graminea*, may be in the form of an upright cylinder, somewhat wider and slightly concave in the upper surface. Large sponges of this type in the Gulf of Mexico waters, however, are usually cup-shaped. Other sponges sometimes found are the reef sponge, *Spongia officinalis* ss. *obliqua*. These are small sponges somewhat cylindrical in general shape but with lobes terminated by oscula on the upper surface. The glove sponge, assigned to *Spongia graminea*, is stoutly columnar with fluted sides. The shape and appearance varies considerably according to the environment. Detailed descriptions of the various forms are given by Moore (1910).

The outer surface is covered with a thin but tough skin which is usually dense black in color. Portions of the sponge buried in mud and the basal portions are more or less deficient in pigment. The flagellated chambers of all commercial sponges are small in size and are pyriform or subspherical in shape with a diameter of no more than 0.03 mm. The choanocytes are approximately 4 microns in cross section.

Spongin fiber has been analyzed by Block and Bolling (1939). It is composed of keratin, an inert product related to the collogens. Keratin contains iodine and the amino acids lysine, arginine, cystine, phenylalanine, and glycine. Very small amounts of histidine and tyrosine are also present.

Sexual reproduction takes place at all times of the year but most intensively during April, May, and June, and in November and December, according to observations made by the author in the Bahamas Islands. Eggs are found in sponges as small as 2 inches in diameter. They are imbedded in the tissues between the flagellated chambers and are about 0.25 cm. in diameter. In their early stages of development they are white but become a dark olive green as the embryo develops. Whereas eggs are easily visible to the naked eye when a sponge is sliced open, the spermatozoa are not recognizable except under the microscope. No information is available as to whether spermatozoa and eggs are produced by the same sponge at different times. Since they have not been observed in the same sponge at the same time, it is possible that commercial sponges are dioecious.

Toward the end of embryonic development the embryo develops a circle of cilia at the anterior, less strongly pigmented end. The larva then escapes into the excurrent canal system and thence to the exterior. Further development has not been observed in detail in commercial sponges.

There is little definite evidence as to the food of sponges. Ingestion of carmine particles by the choanocytes has been observed by Bidder (1896) and subsequent authors, in the non-commercial sponges. According to Bidder, the flagellated cells of *Sycon raphanus*, which are 5 microns in width, contain rod-shaped bodies similar to bacilli between 1 and 2 microns long. Pourbaix (1931) describes the transference of carmine grains from choanocytes to adjacent amoebocytes. Pourbaix (1931) also states that after feeding with carmine, granules of this appeared in the amoebocytes of the Tunisian commercial sponge.

[1] Contribution No. 109 from the Marine Laboratory, University of Miami.

It seems fairly certain that any solid food used by the sponge must be very small in size and that it is carried into the flagellated chambers by the internal water circulation. The large quantities of bacteria found in the calcareous muds of the Bahamas in the vicinity of commercial sponges suggests that these organisms may be an important constituent of the food of these sponges. It has been suggested, however, that sponges may also be able to absorb dissolved organic nutrients.

Very little is known about the physiology of commercial sponges. Bidder (1923), Parker (1914), and others have studied the water currents. These are set up by movements of the flagella of the choanocytes. These appear to operate independently of each other. The enormous number of flagellated chambers provides the energy whereby a considerable volume of water is pumped through the sponge. In noncommercial species, such as *Spinosella*, it has been shown that although the volume of water is great, the pressure does not amount to more than 5 mm. in height of water. The jet stream leaving the osculum may be detected at several inches distance and is sufficient so that on a calm day a distinct disturbance of the water surface may be seen above commercial sponges which are near to the surface. The oscula may be closed by muscular action when stimulated locally.

Bergmann (1949) and his associates have described in a series of papers the extraction of sterols from sponges. There is a considerable degree of specificity in the type of sterol found in various sponges, and this bears a close relation to taxonomic classification. Although the commercial sponges so far investigated have a high fat content, the sterol content of the unsaponifiable matter is lower than the average. The sterols of commercial sponges have not yet been analyzed in detail.

Commercial sponges are typically found associated with muddy bottom sediments, particularly where rocky outcrops or reefs provide a suitable substrate upon which the larva can settle without being destroyed by silt. They are sometimes found growing attached to dead corals or gorgonians and may occasionally grow upon living green algae, such as *Penicillus*. Under these conditions the alga may eventually become completely imbedded in the sponge except for the lower portion of its stalk.

Commercial sponges appear to flourish where there is a good flow of water but not under very exposed conditions. They are rarely found upon bottoms consisting entirely of rock or, of course, sediments. In the Gulf of Mexico they are found down to a depth of at least 150 feet and in water close to low tide mark. They are not tolerant to reduced salinity except for short periods. They appear to be more resistant to temperature changes, however.

A considerable number of other organisms are associated with sponges. The surface is frequently covered with encrusting Bryozoa and colonial tunicates. All species of the piling fauna normally found in the vicinity may be epizoic upon commerical sponges. The green alga, *Batophora oerstedi*, and species of *Acetabularia* also become attached to the sponge surface. The starfish, *Echinaster*, is sometimes observed upon sponges which have lesions of the outer skin, but it is not certain to what extent the damage is caused by this animal. Nudibranchs are sometimes found in small pits or irregularities of the surface, and it is possible that they may feed upon the sponge tissue. Larger holes may be inhabited by various species of small crabs. *Dromia* is often a permanent inhabitant of such places. The green alga, *Dictyosphaeria favulosa*, grows in convenient niches and may become almost enclosed by the subsequent growth of the sponge. A number of the smaller and commoner gastropods are also found inhabiting cavities of the sponge surface which may have been caused by local necrosis, the activities of carnivores or overgrowth of the sponge around sedentary organisms. The barnacle, *Balanus declivis*, which is more commonly found in noncommercial species of sponges, is occasionally seen imbedded in the surface of commercial types.

A considerable fauna inhabits the larger passages of the canal system. Pearse (1934) lists a large number of organisms inhabiting a reef sponge at Dry Tortugas. The most commonly found in all commercial sponges are the snapping shrimp, *Synalpheus brooksi*, and the polychaete worm, *Leodice spongicola*. Other species of polychaetes are also found, particularly syllids and occasionally *Amphitrite*.

Among other Crustacea occurring here are the pontonid shrimp, *Coralliocaris pearsei*, and numerous amphipods of the genera, *Leucothoe* and

Colomaestix. The stomatopod, *Gonodactylus oerstedi*, and small crabs may inhabit the larger passages.

Ophiuroids, particularly *Ophiactis savigny*, are found both in surface depressions and in the larger portions of the canal system. The anemone, *Aiptasia*, appears to form depressions in the surface of sponges into which it is able to retreat.

The most destructive organism is apparently a species of fungus which caused widespread and intensive mortality among the Gulf of Mexico and Caribbean sponges in 1939. Galtsoff (1940) tentatively identifies the organism as *Spongiophaga communis* which was first observed to be parasitic upon sponges by Carter (1878). Since it was not possible to culture the organism, it cannot definitely be assigned to any particular group of fungi. Further accounts of this sponge disease are also given by Walton Smith (1941) and by Osorio-Tafall (1945).

A number of observations have been made by Galtsoff, Wilson, and others, upon the ability of disassociated sponge cells to re-aggregate. This earlier work is also referred to by de Laubenfels (1934) in experiments upon the regeneration of *Iotrochota*.

The growth rate of sponges has been measured by Crawshay (1939) who measured the increase in size of small cuttings sliced from commercial sponges. He found that the velvet sponge grows at such a rate as to approximately double or treble its volume in the period of a year. Extensive unpublished series of measurements by the present author have shown that the growth expressed as a percentage of size diminishes with increasing size in the case of both sheepswool and velvet sponges. When these sponges reach approximately 12 inches in diameter the central portion of the upper surface begins to undergo local necrosis so that the larger sizes become somewhat doughnut-shaped. This is apparently due to the loss of efficiency in respiratory, excretory, and nutritive exchanges related to a diminution in the surface/volume ratio.

The increase in percentage growth rate with decreasing size makes it possible to cultivate sponges by cutting them into small pieces and by planting each piece upon a stone or cement base. Regeneration of the cut surfaces takes place rapidly, and the sponge quickly attaches itself to the stony surface. Other methods used in sponge cultivation are described by Smith (1949), Moore (1910b), Crawshay (1939), and Cahn (1948).

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HYDROIDS OF THE GULF OF MEXICO

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The life cycle of hydroids "typically" alternates between a sessile, asexually reproducing polyp or hydroid stage and a free-swimming sexual medusa stage. One generation or the other may be reduced, however, or even suppressed entirely. Because of this fact and because hydroids are obtained by shore collectors or by dredging, whereas medusae form part of the plankton and are studied by different zoologists, the taxonomy of the group is in an unhappy state.

Closely related types may differ in a respect that at first sight would appear fundamental: the polyp may produce free-living medusae, or the medusa may remain permanently attached to the polyp, even degenerating completely except for its sex products, which then appear to be the sex products of the polyp. This distinction, far from being of subordinal rank, may split a genus down the middle or, at most, may divide closely related genera from each other, according to one's view of what constitutes a generic character. That is, unless the structural characters of the hydroid are to be given no weight whatever, the mode of reproduction cannot provide the basis for erecting taxonomic categories higher than the genus.

Thus, the hydrozoan systematist faces a real dilemma, and he is not helped by the fact that many typically reproducing species have received different names as medusae and as polyps and must continue to bear them until proof of their identity is obtained. The writer is not a student of medusae, and in fact his knowledge of hydroids is largely confined to specimens preserved in alcohol. He is in no position to do anything about the fact that even the families are differently constituted in hydroid and medusa systematics, and the task of fusing the two systems awaits an abler zoologist. This chapter deals exclusively with hydroids.

The hydroid fauna of the Gulf of Mexico is little known, and the chief purpose of this account is to document this fact. A treatise on the Gulf of Mexico is a peculiarly appropriate setting for such a catalog of ignorance, for what we do not know about Gulf hydroids should be especially obvious against the massive backdrop of what we know about the biology of the Gulf.

COLLECTING

Hydroid collecting in the Gulf of Mexico has been chiefly undertaken in the Tortugas and the Florida Keys, but if we except the work of Mayer (1910) as dealing almost entirely with medusae, the only paper specifically discussing the Tortugas fauna is that of Wallace (1909). Gulf of Mexico records are scattered through many papers (Fraser 1943, 1945; Jäderholm 1896, 1903, 1920; Leloup 1935, 1937; Perkins 1908; Pourtalès 1869; Stechow 1912, 1919, 1923, 1926) and through the monographs of Nutting (1900, 1904, 1915), but systematic dredging in the region has not been undertaken since the days of the *Corwin* and the *Blake*. The collections of L. de Pourtalès on the former vessel were reported by Allman (1877), and those of A. Agassiz on the latter were published by Clarke (1879) and Fewkes (1881).

The monograph of Fraser (1944) recapitulates all the earlier records and adds many more, for Fraser examined the large collections in the U. S. National Museum and the Museum of Comparative Zoology whither most of the American hydroids collected in the nineteenth century eventually made their way. It is possible to extract from Fraser's book an essentially complete picture of the hydroid fauna of the Gulf as far as it is known. In fact, this procedure is the basis of the present account. Fraser's list has been expanded in only one noteworthy respect. The survey of fouling on navigation buoys, conducted by the Woods Hole Oceanographic Institution during World War II, yielded several hundred records of hydroids from the Bahamas, both coasts of Florida, and Texas. Most of these are still unpublished, but those that are new

records from the Gulf proper are starred in the check list. The Texas records are of exceptional interest, however, as only three hydroids had previously been recorded from those waters; they were included in the writer's account of the hydroids of Louisiana and Texas (Deevey 1950), a zoogeographic discussion that was founded primarily on a small collection made by J. W. Hedgpeth.

ZOOGEOGRAPHY

The list of 183 species looks impressive, but it would be idle to pretend that the hydroids of the Gulf are well-known. Tropical regions generally have a wealth of species, but hydroid habitats are probably no more extensive in the tropics than elsewhere. The rarity of the rarest species is correspondingly greater, and it is unlikely that more than half the hydroids living in the Gulf have yet been found there. Partly because of inadequate collecting and partly because shallow water hydroids are always under suspicion as fouling organisms, little can be said about the meaning of their geographic distribution.

Of the total of 183 hydroid species known from the Gulf of Mexico, 95 are also found in the Caribbean and another 18, though not yet recorded from the Caribbean, are known from the eastern tropical Pacific. The remaining 70 species include some of the most interesting.

Some of the 70, of course, are known only from the Gulf, but while a few true endemics are to be expected it is too early to say which ones they are; at any rate, no common species is known to be endemic. The interesting members of the group of 70 are those whose main range is otherwise boreal. The boreal species among the hydroids of Texas and Louisiana have already been discussed (Deevey 1950). They include several, such as *Podocoryne carnea*, that are unknown in the warmer parts of the Gulf, and at least one, *Tubularia crocea*, whose ecology is well enough understood to indicate that it could not flourish in southern Florida. To the list of supposed relicts of a glacial age of the Pleistocene given in the earlier paper may be added the name of *Cladocarpus flexilis*, a moderately deep water species taken at three stations off Mobile but not otherwise known south of Cape May. In several other cases we have the familiar phenomenon of a shallow water boreal species occurring at considerable depths in the Gulf (and Caribbean): *Eudendrium tenellum*, *Lafoea dumosa*, *L. gracillima*.

Another way of looking at the facts is this: of 156 species known from the Caribbean, 61 are not known from the Gulf; 29 of them, at least, are common enough in the Caribbean to have been taken at more than one station. Hydroid statistics are scarcely necessary to prove the point, but it is obvious that the Gulf is not a strictly tropical body of water. Low winter temperatures and low and variable salinity, particularly along the northwestern shore, are only some of the factors that must be responsible for maintaining a different "fauna" in the Gulf of Mexico.

The 95 species that are common to the Gulf and the Caribbean present different problems. Most of them are definitely warm water types, although a high proportion belong to the tropical flotsam (especially sargassum) fauna and so may not be true residents of the Gulf. Seventy of the Gulf hydroids and 59 of the 156 Caribbean species are represented in the much larger list of 312 species recorded from the eastern tropical Pacific. The richness of the Pacific fauna, which is known almost exclusively from the Allan Hancock collection (Fraser 1948), is another indication that the Caribbean hydroids have been inadequately collected; it is surely correct to suppose that the 18 species common to the Gulf and the eastern tropical Pacific will appear in the Caribbean, along with many others. What is surprising is that nearly half of the tropical Atlantic hydroids cross the Isthmus of Panama without undergoing specific differentiation. If one cares for statistical statements, the "strength of the relationship" between the Gulf and Pacific faunas is nearly as great (38 percent) as is that between the Gulf and Caribbean faunas (52 percent).

The Isthmus of Panama is not very old, and many biogeographers have supposed that it is younger than most of the species of marine organisms (Schuchert 1935). The problem is related to that of Tethyan distributions; pan-tropical species (more usually genera) are supposed to have had their ranges established in the Tethys Sea, of Cretaceous and early Tertiary age, only to have them sundered by the rise of central Asia (see Ekman 1934, 1935, for review). If disjunct distributions in the Mediterranean and the

Indian western Pacific regions have had this origin, there is no reason to doubt that the Isthmus of Panama was crossed about the same time by the same species, or some of them. The species that are perhaps most likely to have spread so widely and to have crossed modern land barriers so freely are now truly pan-tropical species, but the evidence they provide, according to the conventional canons of biogeography, is ruled invalid by the possibility that they are spreading today. Unhappily, if one chooses to follow the rules and exclude the pan-tropical species, it can only be said that the remaining species prove nothing, at least as far as hydroids are concerned. The reason is not so much biogeographic as taxonomic.

The number of hydroids common to the two sides of Central America is large, but an even larger number is common to the two coasts of North America taken as a whole. According to Fraser's tabulation (1944), 123 species are known from east and west coasts of the Americas, and by no means all of these are circumpolar. Neither are the tropical species all pan-tropical. The "American" distribution pattern is far too common to be accidental, but its commonness raises doubts about the taxonomy. Fraser was a sound, careful worker with a "good eye" for specific differences. However, his experience, though enormous, was largely confined to the Americas. When one remembers that the hydroids of the East Indies are poorly known (only three families of the *Siboga* hydroids having been reported by Billard before his death), one cannot escape the suspicion that many species apparently endemic to the American tropics are still to be collected, or are already known under other names, from other parts of the world. Apart from this taxonomic difficulty, inadequate knowledge of the hydroids of the western Pacific and Indian Oceans imposes another limitation on the case for Tethyan paleogeography, for western Atlantic–western Pacific disjunctions have often been used (however unwisely) in building such a case, and we know of no certain examples among hydroids.

Until the hydroids of the world have been given much more study and some monographic revision, then, it is unsafe to use them for many zoogeographic purposes.

CHECK LIST OF GULF OF MEXICO HYDROIDS

Geographic distribution is indicated by the following symbols:

K, Florida Keys, including Cay Sal Bank and southern Florida as far east as Miami, but not the Bahamas.

T, Tortugas.

C, Cuba.

Y, Yucatán.

NW, northwestern Gulf (Texas, Louisiana).

NE, northeastern Gulf (including Tampa Bay).

Ca, Caribbean Sea.

EP, eastern tropical Pacific Ocean, south of United States-Mexico boundary, and including the oceanic islands.

*, starred names are new records for the Gulf of Mexico, found in the Woods Hole Oceanographic Institution fouling collection.

Suborder GYMNOBLASTEA (Anthomedusae), athecate hydroids

Cordylophora lacustris Allman, 1844. NW; Ca.
Turritopsis fascicularis Fraser, 1943. K.
**Turritopsis nutricula* McCrady, 1856. K; Ca, EP.
Syncoryne eximia [1] (Allman, 1859). NW.
Syncoryne mirabilis L. (Agassiz), 1862. K; EP.
Zanclea costata Gegenbaur, 1856. T, NW; Ca, EP.
Zanclea gemmosa McCrady, 1858. T; EP.
Bimeria franciscana Torrey, 1902. NW; B.
Bimeria humilis Allman, 1877. T, NW; Ca.
Bougainvillia carolinensis (McCrady, 1858). T, NW.
Bougainvillia inaequalis Fraser, 1944. NW.
Bougainvillia rugosa Clarke, 1882. NW; Ca.
Eudendrium album Nutting, 1898. K; EP.
Eudendrium attenuatum Allman 1877. T; EP.
Eudendrium carneum Clarke, 1882. T; Ca, EP.
Eudendrium distichum Clarke, 1879. K.
Eudendrium exiguum Allman, 1877. K; Ca, EP.
Eudendrium eximium Allman, 1877. K, NE; EP.
Eudendrium fruticosum Allman, 1877. K.
Eudendrium gracile Allman, 1877. K.
Eudendrium hargitti Congdon, 1906. T.
Eudendrium laxum Allman, 1877. K; Ca.
Eudendrium speciosum Fraser, 1945. NE.
Eudendrium tenellum Allman, 1877. K; Ca, EP.
Eudendrium tenue A. Agassiz, 1865. NW?; Ca, EP.
Hydractinia echinata Fleming, 1828. K, NW.
Podocoryne carnea Sars, 1846. NW.
Pennaria tiarella (Ayres, 1854). K, T, C; Ca, EP.

[1] N. J. Berrill, in a letter to the author, has given good reasons for suspecting that the species reported under this name from Texas and from western Florida (Deevey 1950), is an undescribed species.

Ectopleura grandis Fraser, 1944. K, NW.
Tubularia crocea (L. Agassiz, 1862). NW; EP.
Cladonema mayeri Perkins, 1906. T.

Suborder CALYPTOBLASTEA (Leptomedusae), thecate hydroids

Family CAMPANULARIDAE

Campanularia amphora (L. Agassiz, 1862). T?
Campanularia (?) *brevicaulis* Nutting, 1915. Y.
Campanularia flexuosa (Hincks, 1861). T?
**Campanularia* (?) *hummelincki* (Leloup, 1935). K; Ca.
Campanularia (?) *macroscypha* Allman, 1877. K, T, Y.
Campanularia marginata (Allman, 1877). K, T, C; Ca.
Clytia coronata (Clarke, 1879). K, NW; Ca, EP.
Clytia cylindrica L. Agassiz, 1862. K, NW; Ca, EP.
Clytia fragilis Congdon, 1907. T, NW; Ca.
Clytia johnstoni (Alder, 1856). K, T; EP.
Clytia longicyatha (Allman, 1877). K, T, NW; Ca, EP.
Clytia macratheca (Perkins, 1908). K, T; Ca.
Clytia minuta (Nutting, 1901). T?
Clytia noliformis (McCrady, 1858). T, NW; Ca, EP.
**Clytia raridentata* (Alder, 1862). K; Ca, EP.
Gonothyraea gracilis (Sars, 1851). K, NW; Ca, EP.
Obelia bicuspidata Clark, 1876. K, NW, NE; Ca.
Obelia commissuralis McCrady, 1858. T?; EP.
Obelia dichotoma (Linnaeus, 1758). K, T, C, NW, NE; EP.
Obelia equilateralis Fraser, 1938. NW; Ca, EP.
Obelia geniculata (Linnaeus, 1758). NW; Ca, EP.
Obelia hyalina Clarke, 1879. K, C; Ca, EP.
Obelia obtusidens (Jäderholm, 1904). NW; EP.

Family CAMPANULINIDAE

**Cuspidella costata* Hincks, 1868. K.
Cuspidella humilis (Alder, 1862). NW; EP.
Eucuspidella pedunculata (Allman, 1877). T.
**Lafoeina tenuis* Sars, 1873. K, NE.
Oplorhiza parvula Allman, 1877. K.
Stegopoma fastigiata (Alder, 1860). T.
Thyroscyphus ramosus Allman, 1877. K, T; Ca.

Family HALECIDAE

Halecium bermudense Congdon, 1907. K, T, NE; Ca, EP.
Halecium dyssymetrum [2] Billard, 1929. K, T.
Halecium filicula Allman, 1877. K.
Halecium gracile Verrill, 1874. K; EP.
Halecium macrocephalum Allman, 1877. K, T; EP.
Halecium nanum Alder, 1859. K, T, NW; Ca, EP.
Halecium tenellum Hincks, 1861. T, NE; Ca, EP.

Family HEBELLIDAE

Hebella calcarata (A. Agassiz, 1865). NE; Ca, EP.
Scandia mutabilis (Ritchie, 1907). T; Ca, EP.

[2] Preliminary study of this species in the Woods Hole Oceanographic Institution fouling collection indicates that it is probably the *H. dyssymetrum* of Leloup (1935) but not of Billard, and that it needs a new name.

Family LAFOEIDAE

Acryptolaria abies (Allman, 1877). K; Ca.
Acryptolaria conferta (Allman, 1877). T, C; Ca, EP.
Acryptolaria elegans (Allman, 1877). K, T; Ca.
Acryptolaria longitheca (Allman, 1877). K, T; Ca.
Acryptolaria pulchella (Allman, 1888). K; EP.
Eucryptolaria pinnata Fraser, 1938. C; Ca, EP.
Filellum serpens (Hassall, 1852). T, NW; Ca, EP.
Filellum serratum (Clarke, 1879). C; Ca.
Lafoea coalescens Allman, 1877. K.
Lafoea dumosa (Fleming, 1828). T; Ca, EP.
Lafoea gracillima (Alder, 1857). T; Ca, EP.
Lafoea tenellula Allman, 1877. K; Ca.
Lafoea venusta Allman, 1877. K, T, C; Ca.
Lictorella convallaria (Allman), 1877. K, T, C; Ca, EP.
Zygophylax rigida (Fraser, 1940). Y.

Family SYNTHECIDAE

Synthecium ? *gracile* Fraser, 1937. T; Ca, EP.
Synthecium ? *marginatum* (Allman, 1877). K; Ca.
Synthecium ? *nanum* Fraser, 1943. T; Ca.
Synthecium ? *rectum* Nutting, 1904. C.
Synthecium tubithecum (Allman), 1877. K, T, C; Ca.

Family SERTULARIDAE

Diphasia digitalis (Busk, 1852). K, T, C; Ca.
Pasya quadridentata (Ellis and Solander, 1786). T, NW; Ca, EP.
Sertularella amphorifera Allman, 1877. K, T, C, Y; Ca, EP.
Sertularella areyi Nutting, 1904. C.
Sertularella conica Allman, 1877. K, T, NW, NE; Ca, EP.
Sertularella distans (Allman, 1877). T, C, Y; Ca.
Sertularella formosa Fewkes, 1881. C; Ca, EP.
Sertularella gayi (Lamouroux, 1821). K, C, Y, NW; Ca.
Sertularella humilis Fraser, 1943. K.
Sertularella megastoma Nutting, 1904. Y; Ca.
Sertularella pinnigera Hartlaub, 1900. K; Ca.
Sertularella quadrata Nutting, 1904. C; Ca.
Sertularella sieboldi Kirchenpauer, 1884. C.
Sertularella speciosa Congdon, 1907. K; Ca.
Sertularella tenella (Alder, 1856). C; Ca, EP.
Sertularia cornicina (McCrady, 1858). K?, Y; Ca, EP.
Sertularia dalmasi (Versluys, 1899). T, NW, NE; Ca, EP.
Sertularia exigua Allman, 1877. K; Ca, EP.
Sertularia flowersi Nutting, 1904. C.
Sertularia inflata (Versluys, 1899). K, T, NW, NE; Ca, EP.
Sertularia mayeri Nutting, 1904. K, T; Ca, EP.
Sertularia pourtalesi Nutting, 1904. K, T; Ca, EP.
Sertularia stookeyi Nutting, 1904. K; EP.
Sertularia tumida Allman, 1877. T.
Sertularia turbinata (Lamouroux, 1816). K, T; Ca.
Thuiaria crisioides (Lamouroux, 1824). K; Ca, EP.
Thuiaria tropica (Stechow, 1926). T.
Idiella pristis (Lamouroux, 1816). K, T; Ca.

Family PLUMULARIDAE

Aglaophenia allmani Nutting, 1900. K, T; Ca.
Aglaophenia aperta Nutting, 1900. C, NE.
Aglaophenia bicornuta Nutting, 1900. C.
Aglaophenia ? constricta Allman, 1877. K.
Aglaophenia cristifrons Nutting, 1900. C, NW.
? Aglaophenia dichotoma Kirchenpauer, 1872. NE.
Aglaophenia dubia Nutting, 1900. K, T, C; Ca, EP.
Aglaophenia elongata Meneghini, 1845. NE.
Aglaophenia flowersi Nutting, 1900. K; Ca.
Aglaophenia late-carinata Allman, 1877. K, T, NW; Ca.
Aglaophenia longiramosa Fraser, 1945. NE.
Aglaophenia lophocarpa Allman, 1877. K, T, C, NE; Ca, EP.
Aglaophenia ? mercatoris Leloup, 1937. NE.
Aglaophenia perpusilla Allman, 1877. K, T, NW; Ca.
Aglaophenia raridentata Fraser, 1944. K.
Aglaophenia rhynchocarpa Allman, 1877. K, T, C; Ca.
Aglaophenia rigida Allman, 1877. K, NW; Ca, EP.
Aglaophenia tridentata Versluys, 1899. K, T; Ca.
Aglaophenoides mammillata (Nutting, 1900). T.
Aglaophenopsis hirsuta Fewkes, 1881. K.
Antennella gracilis Allman, 1877. K, C; Ca, EP.
Antennella quadriaurita Ritchie, 1909. K, C.
Antennella secundaria (Gmelin, 1788). T; Ca.
Antennopsis distans Nutting, 1900. C.
Antennopsis hippuris Allman, 1877. K.
Antennopsis longicorna Nutting, 1900. C.
Antennopsis nigra Nutting, 1900. C.
Antennularia simplex Allman, 1877. K, C.
Cladocarpus carinatus Nutting, 1900. T.
Cladocarpus dolichotheca Allman, 1877. K, T.
Cladocarpus flexilis Verrill, 1885. NE.
Cladocarpus flexuosus Nutting, 1900. NE.
Cladocarpus longipinna Fraser, 1945. NE.
Cladocarpus obliquus Nutting, 1900. C.
Cladocarpus paradisea Allman, 1877. K.
Cladocarpus sigma (Allman, 1877). K, C.
Cladocarpus tenuis Clarke, 1879. T; Ca.
Cladocarpus ventricosus Allman, 1877. K.
Diplopteron longipinna Nutting, 1900. K.
Diplopteron quadricorne Nutting, 1900. C; Ca.
Halicornaria sinuosa Fraser, 1925. K, NE.
Halicornaria speciosa Allman, 1877. K; Ca.
Halopteris carinata Allman, 1877. K, T; Ca.
Lytocarpus clarkei Nutting, 1900. C, Y; Ca.
Lytocarpus grandis (Clarke, 1879). K; Ca.
Lytocarpus philippinus (Kirchenpauer, 1872). K, T; Ca, EP.
Monostaechas quadridens (McCrady, 1858). K, T, Y; NW, NE; Ca, EP.
Plumularia attenuata Allman, 1877. K; Ca, EP.
Plumularia clarkei Nutting, 1900. C.
Plumularia diaphana (Heller, 1868). K, T, NW; Ca, EP.
Plumularia filicula Allman, 1877. K; EP.
Plumularia floridana Nutting, 1900. K, T, NW; EP.
Plumularia geminata Allman, 1877. K; Ca.
Plumularia inermis Nutting, 1900. T; Ca, EP.
Plumularia macrotheca Allman, 1877. C.
Plumularia margaretta (Nutting, 1900). K, T; Ca, EP.
Plumularia megalocephala Allman, 1877. K, C; Ca, EP.
Plumularia paucinoda Nutting, 1900. C.
Plumularia setacea (Ellis, 1755). K, T, NW, NE; EP.
Plumularia setaceoides Bale, 1882. K, Ca.
Plumularia strictocarpa Pictet, 1893. K; Ca.
Schizotricha dichotoma Nutting, 1900. K.
Schizotricha tenella (Verrill, 1874). NW?; Ca, EP.
Thecocarpus bispinosus (Allman, 1877). K.
Thecocarpus distans (Allman, 1877). K, T.

SUMMARY

A total of 183 species of hydroids, 31 athecate and 152 thecate, are known from the Gulf of Mexico, mostly from the Tortugas and the Florida Keys. Medusae are not considered. The Gulf and the Caribbean have 95 species in common, but 61 Caribbean species are unknown in the Gulf. Seventy Gulf species also occur in the eastern tropical Pacific, including 18 not yet known from the Caribbean. Taxonomic difficulties, as well as inadequate collecting, make hydroid geography an unsatisfactory subject, and it is uncertain how far the apparently common "American" distribution pattern should be taken seriously. What is especially interesting is the occurrence in the Gulf of a significant number of boreal species, some of them seemingly disjunct in the northwestern Gulf.

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HYDROMEDUSAE OF THE GULF OF MEXICO

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So few plankton collections have been made in the Gulf of Mexico and so few of these have been studied by hydromedusae specialists that it is necessary to rely almost entirely on Mayer's (1900, 1904, 1910) reports from the Tortugas. It is to be noted that most names listed in Mayer's first (1900) paper were reduced to the synonomy of other species in his monograph of 1910. Subsequent writers, expecially Bigelow (1913, 1918, 1919, 1938, 1940), Kramp (1919, 1920, 1926, 1930, 1932, 1933, 1939, 1942, 1947, 1948), and Ranson (1936) have also made certain revisions resulting in a slight reduction in the number of species originally enumerated by Mayer in his monograph (1910).

In comparing the resulting list with that in the section on the hydroids it is striking to note that few species (i. e., *Turritopsis nutricula* McCrady, *Zanclea costata* Gegenbaur, *Bougainvillia carolinensis* McCrady, *Pennaria tiarella* McCrady, and *Cladonema mayeri* Perkins among the Anthomedusae) appear on both lists. In large part this is due to the fact that many hydroids do not liberate free-swimming medusae, and that many medusae have very much reduced hydroid stages. Indeed, in many instances the hydroid stage is completely unknown, if it exists.

Insofar as it has been possible to determine only about 70 species have been recorded (30 Anthomedusae, 34 Leptomedusae, 5 Trachymedusae, and 3 Narcomedusae) from the Gulf of Mexico region. Some of these, not already mentioned above, are good species also known elsewhere:

Corymorpha nutans Hartlaub; *Hybocodon forbesii* Mayer; *Sarsia mirabilis* L. Agassiz; *Ectopleura minerva* Mayer; *Dipurena ophiogaster* Haeckel; *Zancleopsis dichotoma* Mayer; *Amphinema dinema* Péron et LeSueur; *A. octaedra* Haeckel; *A. rugosa* Mayer; *A. turrida* Mayer; *Merga violacea* Agassiz and Mayer; *Podocoryne minuta* Trinci; *Lymnorea alexandri* Mayer; *Bougainvillia niobe* Mayer; *Köllikerina elegans* Mayer; *Proboscidactyla ornata* McCrady, among the Anthomedusae; *Laodicea cruiciata* Forskål; *Phalidium discoida* Mayer; *Phialucium carolinae* Mayer; *Eucheilota ventricularis* McCrady; *E. duodecimalis* A. Agassiz; *Eutima mira* McCrady; *E. elephas* Haeckel; *Eutimalphes coerulea* L. Agassiz; *Phortis pyramidalis* L. Agassiz; *P. lactea* Mayer; *Aequorea floridana* Mayer, among the Leptomedusae; *Geryonia proboscidalis* Forskål; *Liriope tetraphylla* Chamisso and Eysenhardt; *Olindias phosphorica tenuis* Fewkes; *Rhopalonema velatum* Gegenbaur, among the Trachymedusae; and *Aeginura grimaldii* Maas; *Cunoctantha octonaria* McCrady; *Solmundella bitentaculata* Quoy and Gaimard (using the names which appear to conform with present usage).

A goodly number of species, however, do not appear to have been subject to critical review in recent years, so that it is uncertain whether they are good species or merely synonyms of others. Hence, they are not listed at this time.

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SIPHONOPHORES IN THE GULF OF MEXICO

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The siphonophores most often recorded from the Gulf of Mexico are the two large conspicuous species with floats above the surface of the water, *Physalia physalis* L. and *Velella velella* L. Possibly *Porpita umbella* O. F. Muller [1] should also be included with these (Whitten, Rosene, and Hedgpeth, 1950). As early as 1886, Fewkes wrote, "I have many new localities for this medusa [i. e., *Velella*] in the Gulf of Mexico." The *Atlantis* in the winter of 1951 sailed through swarms of *Physalia* together with large quantities of *Velella* some miles in extent (Stetson, personal communication) out in the Gulf off the northwest coast of Florida, and newspapers give frequent account of the contamination of west Florida bathing beaches.

The smaller, more common species, however, have scarcely been noted in the Gulf except at a few localities around its periphery, chiefly at the Tortugas (Mayer 1900) and in adjacent bodies of water such as the Straits of Florida (Bigelow 1918), the Caribbean (Fewkes 1889), and the Gulf Stream proper (Bigelow 1918; Fewkes, 1882, 1886, 1889). These records are indicative that about 25 of the better known species in all probability occur in the Gulf of Mexico proper:

> *Abyla carina* Haeckel; *Abylopsis tetragona* Otto; *A. eschscholtzii* Huxley; *Agalma okeni* Eschscholtz; *Amphicaryon acaule* Chun; *Bassia bassensis* Quoy and Gaimard; *Ceratocymba sagittata* Quoy and Gaimard; *Chelophyes appendiculata* Eschscholtz; *Diphyes bojani* Chun; *Diphyes dispar* Chamisso and Eysenhardt; *Enneagonum hyalinum* Quoy and Gaimard; *Eudoxoides spiralis* Bigelow; *Galetta australis* Quoy and Gaimard; *Hippopodius hippopus* Forskål; *Lensia fowleri* Bigelow; *Rhizophysa eysenhardti* Gegenbaur; *Rhizophysa filiformis* Forskål; *Sphaeronectes truncata* Will; *Stephanomia rubra* Vogt; *Sulculeolaria monoica* Chun; *Sulculeolaria quadridentata* Quoy and Gaimard; *Vogtia glabra* Bigelow; *Vogtia pentacantha* Kölliker (as they are now named).[2]

In the Gulf of Mexico, one might expect to find possibly 50 other species of Calycophorae, which have been taken in the tropical Atlantic and perhaps as many more among the Physophorae, Rhizophysaliae, and Chondrophorae combined. Most of these species have been taken at one time or another in the tropical Atlantic and might be expected to be carried by the currents into the Gulf of Mexico. The depth of the sill at the entrances to the Caribbean and Gulf of Mexico is sufficiently great to permit entry of even the species that live at considerable depths, a factor which, for example, apparently prevents some siphonophore species from entering the Mediterranean (Bigelow and Sears 1937).

In short, it would not be surprising to find any one of the 140 or more siphonophore species, now known, in the Gulf of Mexico.

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[1] See Bigelow and Sears (1937) for use of this name.

[2] References which are especially helpful and readily accessible in establishing the accepted names are: Bigelow, 1911a, 1911b, 1913, 1918, 1919, 1931; Bigelow and Sears, 1937; Sears, in press; Totton, 1932, 1941, in press.

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SCYPHOZOA

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With the exception of Mayer's studies at Tortugas nearly 50 years ago there has been no serious attempt to study the medusae of the Gulf of Mexico. While there are a few scattered records of medusae along the coast, little is available on the occurrence of jellyfish in the pelagic regions of the Gulf or of the deep-water forms.

There are a few large medusae which characteristically occur in the neritic waters of the Gulf of Mexico from Florida to the Rio Grande. Foremost of these is *Stomolophus meleagris*, the cabbagehead. This rhizostome often occurs in vast numbers in lower bays and around passes at the end of the summer. Such swarms were observed at Port Aransas, Texas, on August 4–5, 1947, and September 20, 1948. The latter swarm was estimated to be drifting through the channel on an incoming tide at the rate of 2 million an hour. The bobbing white domes of these jellyfish seemed to be packed almost solidly across the 800-yard width of the channel. Occasionally, *Stomolophus* is caught by the ton in shrimp trawls, and there has been some speculation about a possible economic use for these animals. Mayer mentions several oriental species which are pickled, but such a specialty delicatessen use would hardly cut into the unwanted surplus. With the possible exception of a few hypersensitive individuals, *Stomolophus* is not a dangerous species to bathers and may be handled with impunity. It is a fine animal for physiological experimentation.

Another rhizostome, *Rhopilema verrilli*, may be more common than suspected. Specimens have been taken from Mobile Bay, and one was collected at Port Aransas. This is a much larger medusa than *Stomolophus*, and Mayer suggested that it is a southern form which occasionally extends as far north as Long Island. Burkenroad (personal communication) considers it common in Chandeleur Sound.

One of the most common jellyfish in the bays, especially during the summer months, is *Dactylometra quinquecirrha*, a semaeostome medusa. This medusa may cause a mild rash or unpleasant sting,[1] but severe cases of jellyfish poisoning by this species are rarely reported (Hedgpeth 1945).

An occasional denizen of bay waters is the moon jelly, *Aurellia aurita*. While it is usually more a frequenter of the lower bays and gulf waters, it at times outnumbers *Dactylometra* in the bays.

Another large Medusa in Gulf waters is the lion's mane, *Cyanaea capillata* var. *versicolor*. Mayer gives the southern limit of this variety as Cape Canaveral, Florida, and did not find it at Tortugas. R. O. Christenson, of Alabama Polytechnic Institute, identified this medusa from Mobile Bay, on February 20, 1938. A large, reddish, striped medusa was observed on an outgoing tide at Port Aransas, Texas, on March 16, 1948, which appeared to be this species. It is of interest to note that both these records are toward the end of the Gulf coast winter. Burkenroad (personal communication) considers it common in Louisiana waters.

According to Mayer, some 75 species of medusae occur at Tortugas. Nine of these are scyphozoans, and the great majority are hydromedusae, more properly considered under hydroids (p. 267). There are probably more species to be found in the Gulf. Following is a list of the Scyphomedusae known to occur in the Gulf of Mexico, principally at Tortugas. This list includes the 9 species discussed by Mayer and the 2 species whose occurrence in the Gulf was not known to him:[2]

Carybdaea aurifera Mayer, pp. 510, fig. 328.
A rare form taken only twice at Tortugas.

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[1] The Portuguese Man-of-War, *Physalia*, is more dangerous and probably causes some distress to unwary bathers every season. This siphonophore is often washed up on the outer beaches in great numbers, and its stranded pneumatophores are heard popping under the wheels by motorists driving on the beach. Two smaller siphonophores, *Porpita linneana* and *Velella vellela*, are often stranded on the beach.

[2] All page and figure numbers given after the name of the species refer to Mayer's publication, 1910.

Nausithoë punctata Kölliker, pp. 554–556, pl. 60, figs. 4–5, text fig. 352.[1]

This medusae is noteworthy for the peculiar, branched scyphistoma which lives commensally in sponges. Found in all tropical and warm seas.

Linuche unguiculata Eschscholtz, pp. 558–559, pl. 59, figs. 1–10.

A West Indian species. Forms vast swarms in spring in the Florida-Bahama region according to Mayer.

Dactylometra quinquecirrha L. Agassiz, pp. 585–588, pls. 62–64a, text figs. 370–372.

Widely distributed from New England to the tropics; possibly also Pacific. Abundant in Tampa Bay in August (p. 586).

Cyanaea capillata var. *versicolor* L. Agassiz, pp. 600–601, pl. 65, figs. 1–2.

Western Atlantic and Gulf, south of Cape Hatteras.

Aurellia aurita Lamarck, pp. 623–626, pl. 67, figs. 1–4, fig. 4; 68.

In east American waters, common from Greenland to West Indies. World wide.

[1] See footnote 2, page 277.

Cassiopea xamachana R. P. Bigelow, pp. 641–646, pls. 69–72. *C. frondosa* Lamarck. Pp. 647–648, pl. 69 and 72.

These interesting medusae are the subject of several papers in the Tortugas Laboratory series. The first is known from Tortugas and Jamaica; the second is more widely distributed throughout the West Indies.

Rhopilema verrillii (Fewkes), pp. 707–709, pl. 7, fig. 1, text fig. 424.

From New Haven to Port Aransas, but not (?) Tortugas.

Stomolophus meleagris L. Agassiz, pp. 710–711, pls. 75–76.

Abundant along southern Atlantic and Gulf of Mexico (not north of Chesapeake Bay), and West Indies. Also on Pacific side of Isthmus, and north at least to San Diego.

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ANTHOZOA: ALCYONARIA [1]

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The Alcyonaria of the Gulf of Mexico [2] are little known. No systematic work treats them in detail, and the preparation of such an account must await more extensive collections from the entire region. Even papers mentioning occasional Gulf species are few and, with perhaps two or three exceptions, deal only with those found in the extreme southeastern part (i. e., the Straits of Florida, the Florida Keys, and Dry Tortugas). Notable among these is the series of reports by Bielschowsky (1929), Kükenthal (1916), Kunze (1916), Riess (1929), and Toeplitz (1929), published under the general title, Die Gorgonarien Westindiens in the supplement volumes 11 and 16 of the Zoologische Jahrbucher. Professor A. E. Verrill (1864, 1869, 1883) early recorded the presence, mostly in the lower Gulf, of a few alcyonarians; and some later work by Stiasny, especially the two *Siboga* supplements (1935, 1937), adds to the list of species known from the Tortugas area.

Explorations in the Gulf of Mexico have not been extensive, and collections are correspondingly inadequate. The exploratory vessels, *Albatross*, *Fish Hawk*, *Pelican*, *Blake*, *Bibb*, and *Bache* have all made dredge hauls in the Gulf, but the records of only the last three have been published, these in the classic monograph on the alcyonarians of the western Atlantic by Dr. Elisabeth Deichmann (1936). Exploratory trawling is currently being carried on by the U. S. Fish and Wildlife Service M/V *Oregon*, but very few alcyonarians have so far been seen.

Present knowledge of the alcyonarians of the Gulf of Mexico is summarized in the accompanying table (table 1), which also indicates the distribution outside of the Gulf of the species concerned.

TABLE 1.—*Geographical distribution of alcyonarians known from the Gulf of Mexico*

A. Arctic to Cape Cod.
B. C. Cod to C. Hatteras.
C. C. Hatteras to C. Canaveral.
D. Bermuda.
E. C. Carnaveral to Sombrero Key.
a. Low water to 10 fathoms.
b. 10–99 fathoms.
1. Bayer 1949.
2. Bayer 1952.
3. Bielschowsky 1929.
4. Cary 1906.
5. Cary 1918.
6. Deichmann 1936.
7. Gordon 1925.
8. Heilprin 1890.
9. Kükenthal 1916.
F. Sombrero Key to Tortugas Bank; Straits of Florida; N. W. coast of Cuba.
G. C. Sable to Apalachee Bay.
H. Apalachee Bay to Galveston.
c. 100–499 fathoms.
d. 500–999 fathoms.
10. Kükenthal 1919.
11. Kükenthal 1924.
12. Kunze 1916.
13. Moser 1921.
14. de Pourtalès 1868.
15. Riess 1929.
16. Stiasny 1935.
17. Stiasny 1937.
18. Stiasny 1941a.
19. Stiasny 1941b.
I. Galveston to Veracruz.
J. Vera Cruz to C. Catoche.
K. Central Gulf Basin.
L. West Indies.
M. Caribbean Sea.
N. Brazil.
e. 1000 fathoms and deeper.
x. No depth given.
20. Stiasny 1941c.
21. Stiasny 1941d.
22. Thomson 1927.
23. Toeplitz 1929.
24. Verrill 1864.
25. Verrill 1869.
26. Verrill 1883.
27. Verrill 1907.

Species	Arctic to Sombrero Key					Gulf of Mexico						West Indies to Brazil		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
ORDER TELESTACEA														
TELESTIDAE														
Telesto flavula, 2, 6						b		b						
Telesto sanguinea, 2, 6					b	b		b						
ORDER ALCYONACEA														
ALCYONIDAE														
Nidalia occidentalis, 2, 6			b		b	b						b		
NEPHTHYIDAE														
Eunephthya nigra, 2, 6, 14			c		b	c								
Neospongodes agassizii, 6						c						b, c		
Neospongodes portoricensis, 2, 6						c						b, c		

[1] Published with the permission of the Secretary of the Smithsonian Institution.

[2] For the purposes of this summary, the geographical boundaries of the Gulf of Mexico will be taken to include, in addition to the usual land masses, a line drawn from Cape Sable, Fla., due south to the coast of Cuba, and another from Cape San Antonio, Cuba, to Cape Catoche, Yucatán. This delimitation is purely arbitrary and does not coincide with faunistic boundaries

TABLE 1.—*Geographical distribution of alcyonarians known from the Gulf of Mexico*—Continued

Species	Arctic to Sombrero Key					Gulf of Mexico						West Indies to Brazil		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
ORDER GORGONACEA														
SUBORDER SCLERAXONIA														
BRIAREIDAE														
Briareum asbestinum, 5, 6					b	a						a	a	
Diodogorgia ceratosa, 11								"Gulf of Mexico"						
Diodogorgia nodulifera, 2, 6					b	b						b		
Iciligorgia schrammi, 2, 6, 18					b	b						b		
Solenopodium polyanthes, 6, 17						a						a		
Titanideum suberosum, 6			b			b								
SUBORDER HOLAXONIA														
ACANTHOGORGIIDAE														
Acauthogorgia aspera, 2, 6, 26			d			c						b, c		
MURICEIDAE														
Bebryce cinerea, 2, 6						c						b, c		
Bebryce grandis, 2, 6						c		b				b, c	c	
Echinomuricea atlantica, 6						b						b, c		
Muricea laxa, 2, 6					a	b	a, b						c	
Muricea muricata, 6, 11, 15, 27				x	x	a						a		
Muricea pendula, 2, 6, 24			a				b	b						
Muricea spicifera, 6, 7						a						a	a	
Placogorgia mirabilis, 2, 6						c							b	
Placogorgia tenuis, 6, 26						c						b, c		
Scleracis guadalupensis, 2, 6, 15						b		b				b, c		
Scleracis petrosa, 6						c						d		
Swiftia casta, 2, 6, 14, 26			c			c		b						
Swiftia exserta, 2, 6					b			b				b	b	
Swiftia koreni, 2, 6					c	d						c		
Thesea citrina, 6						b								
Thesea grandiflora, 6						b						b		
Thesea plana, 2, 6						b		b	b					
Thesea solitaria, 6, 14					c	c								
Trachymuricea hirta, 6, 11						c						b		
Villogorgia nigrescens, 6						b, c						b, c	c	
PLEXAURIDAE														
Eunicea asperula, 12						a						a	x	
Eunicea calyculata, 12						a						a		
Eunicea lugubris, 16				a		a						a		
Eunicea mammosa, 11, 12, 16						a						a	a	
Eunicea multicauda gordoni, 16						a							a	
Eunicea succinea, 2, 12, 16				a		a	a					a	a	
Eunicea tourneforti, 7, 12, 16, 27				a		a						a	a	
Plexaura dubia, 2, 11				a			a					a		
Plexaura edwardsi, 11, 16				a		a						a		
Plexaura flexuosa, 6, 8, 16, 20, 27				a		a				a		a	a	
Plexaura hartmeyeri, 13						a								
Plexaura porosa, 2, 7, 11							a					a	a	
Plexaurella dichotoma, 11, 12, 16, 27				a		a						x		x
Plexaurella dubrovskyi, 16						a								
Plexaurella heteropora, 12, 16						a						x		
Plexaurella kunzei, 2, 11							a					a		
Plexaurella minuta, 11									"Mexico"					
GORGONIIDAE														
Antillogorgia acerosa, 2, 10, 27				x	a	a	a			b		a	a	
A. acerosa elastica, 3, 21						a							x	
Antillogorgia bipinnata, 3, 6, 24						a						b	a	a
Antillogorgia americana, 2, 6, 27				a		a	a					a		
Gorgonia flabellum, 5, 6, 7, 24, 27				a		a			?			a, b	a	
Eugorgia euryale, 2								b						
Eugorgia medusa, 2								b						
Eugorgia stheno, 2					b			b						
Eugorgia virgulata, 2, 4, 6, 20		a	a				a	a	b					
Leptogorgia behes, 2, 6, 25			a			a	a		a					
Leptogorgia miniata, 2, 6					b	b	b						a	
Leptogorgia setacea, 6, 20			a						a			a		
Pterogorgia anceps, 2, 5, 8, 11, 24					a	a	a			a		a		
Pterogorgia citrina, 5, 11, 27				a	a, b	a						a		
Pterogorgia guadalupensis, 2						a						a		
GORGONELLIDAE														
Nicella guadalupensis, 6						c						b, c	c	
Scirpearia barbadensis, 6						c						b, c		
Scirpearia funiculina, 2, 6						b		b				b, c	b	
Scirpearia grandis, 6, 23, 27				b		b								
CHRYSOGORGIIDAE														
Chalcogorgia pellucida, 1						c								
Chrysogorgia desbonni, 6, 26						c						b, c		
Chrysogorgia elegans, 2, 6, 26						d		c	c			c, d		
Chrysogorgia elisabethae, 2						x						c		
Trichogorgia viola, 6						b								

TABLE 1.—*Geographical distribution of alcyonarians known from the Gulf of Mexico*—Continued

Species	Arctic to Sombrero Key					Gulf of Mexico						West Indies to Brazil		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
SUBORDER HOLAXONIA—Continued														
PRIMNOIDAE														
Caligorgia gracilis, 6						c						b, c		
Caligorgia verticillata, 6, 14						c	b			c		e		
Calyptrophora trilepis, 6, 14						c								
Plumarella pourtalesii, 6, 26			c		b	e						x	c	
Stenella imbricata, 6						d						d		
Thouarella antea, 6						c								
Thouarella goësi, 6						c						c		
ISIDIDAE														
Acanella eburnea, 2, 6, 26						d		d				c, d	c, d	c
Order PENNATULACEA														
RENILLIDAE														
Renilla reniformis, 4, 24			x					a						
Renilla mülleri, 2, 6, 24								a	a			a	a	a
PUNICULINIDAE														
Funiculina quadrangularis, 2, 6, 26	c	c	d					c			e	c, d		
PROTOPTILIDAE														
Protoptilum sp. cf. thomsoni, 2								c	c					
UMBELLULIDAE														
Umbellula güntheri, 2, 6		e									e	d		
Umbellula lindahlii, 6	x	d, e									e	e		
VIRGULARIIDAE														
Virgularia mirabilis, 2, 6	x								a					

This table has been compiled from the literature and from collections in the U. S. National Museum, including unpublished records from the *Albatross*, *Fish Hawk*, and *Pelican* expeditions. Published locality records within the Gulf of Mexico as defined above have been located for 72 species; records of only 9 species from Gulf localities exclusive of the lower Florida Keys and Tortugas have been found. Another 19 species have been added by records in the collections of the U. S. National Museum, bringing the total number of species to 91. These species represent 18 families in 4 of the 6 known orders.

Although little is known of the physiology of the alcyonarians, it is clear that bottom conditions, temperature, salinity, available oxygen, and sedimentation play important parts in limiting their distribution. Limits of tolerance are apparently quite narrow but not equally so for all factors. A solid substrate providing satisfactory conditions for the attachment of larvae is almost universally required among all alcyonarian groups excepting the pennatulids. A very few gorgonacean species are able to live unattached, and a number, especially of the families Chrysogorgiidae and Isididae, can adapt themselves to live on either hard or soft bottom. The few gorgonian species which have been investigated in regard to temperature tolerance (L. R. Cary, Papers from the Dept. of Marine Biology, Carnegie Institution of Washington, v. 12, No. 9, 1918) can withstand from 5° to 9° C. (approximately) above the average maximum surface temperature of the area (at the Tortugas, about 29° C.), but it is unlikely that colonies would establish or thrive outside of a rather limited temperature range. In the absence of experimental evidence, it is impossible to state the limits of the salinity and oxygen variation which the alcyonarians can tolerate. A few species can live in situations where the salinity is occasionally somewhat reduced, but most, including the West Indian reef-dwelling forms, are never found where appreciable dilution regularly occurs. Certain species are limited to outer reef situations, and oxygen may be the critical factor in such cases. As a rule, alcyonarians are not found in continuously muddy waters, but some can tolerate very muddy conditions for short periods.

The reef areas of the Tortugas and lower Florida Keys support a typically West Indian gorgonian assemblage. The predominant families are the

Plexauridae and the Gorgoniidae; while not all of the known West Indian members of these families have been recorded from this area, most are to be expected. This community does not extend northward undiminished for any appreciable distance, although a few of the hardier species range about halfway up the Florida west coast. The scarcity of suitable reef-like situations along this coast seems to account in part for their reduction in numbers, and temperature may be of equal importance in limiting the northward distribution of shallow-water gorgonians. *Antillogorgia acerosa*, *A. americana*, and *Pterogorgia anceps* are characteristic reef forms which extend some distance up the west coast of Florida, and they probably occur wherever there is solid bottom suitable for attachment and permanent support. The predominant West Indian genera of reef-dwelling gorgonians, *Plexaurella*, *Eunicea*, *Antillogorgia*, *Gorgonia*, *Pterogorgia*, and *Phyllogorgia*, are restricted to the warm western Atlantic, while a few, such as *Pacifigorgia* and *Muricea*, are most numerous on the Pacific coast of the middle Americas, and at least one, *Leptogorgia*, is found also in the eastern Atlantic, the Mediterranean, east Africa, and the East Indies.

The alcyonarian fauna of the lower west coast of Florida is thus a decimated West Indian assemblage. To the northward it merges with and soon, perhaps near Tampa, is replaced by a distinctly temperate fauna the predominant gorgonians of which are *Leptogorgia virgulata* and *L. setacea* (both of which are referable (Bayer 1952) to Verrill's genus *Eugorgia*), and *Muricea pendula*. These species are especially abundant along the coast of the Carolinas and south perhaps to northern Florida; *L. virgulata* extends north to New York in moderately deep water, but all three seem to be lacking from the lower east coast of Florida. The short-stemmed sea pansy, *Renilla mülleri*, is common in the northern Gulf and extends southward to Brazil; it likewise occurs along the Pacific Coast from Central America to Chile. It has not been recorded from the Atlantic coast of North America where the only species appears to be *Renilla reniformis*, the common long-stemmed sea pansy. The latter species occurs also in the Gulf of Mexico with a variety extending south to the Straits of Magellan and another in California.

The shallow-water gorgonian fauna of the northern Gulf of Mexico is clearly identical with but discontinuous from that of the Carolina coast. This interrupted distribution pattern has been pointed out by Deevey (Ecology, vol. 31, No. 3, pp. 334–367, 1950) for some hydroids and other invertebrates and is described for fishes in this volume (Rivas, p. 503). Deevey suggests that reduced temperature during periods of glaciation permitted continuity of the cool-water fauna around south Florida, but it would seem fully as plausible that this continuity existed when Florida was submerged and that subsequent dispersal around the peninsula has been prevented by a thermal barrier. Since apparently favorable situations exist all along the east coast of Florida, the southward dispersal of these discontinuously distributed gorgonians is probably not limited by bottom conditions but by some other environmental factor of which temperature seems to be the most likely. In any event, it can hardly be doubted that the present-day distribution reflects a former continuity of the Gulf and Carolina faunas, but a satisfactory explanation must await the study of some group with an extensive fossil record.

Although its southern limit is not known, the shallow water temperate assemblage is probably present along most of the Texas coast, somewhere along the coast of Mexico mingling with and giving way to the hardier elements of the West Indian fauna which encroach upon it from the south. At least one gorgonacean, *Leptogorgia setacea*, extends as far south as the Guianas and Trinidad.

The presence of actively growing coral reefs at Veracruz and along the coast of Yucatán has long been recognized, but the composition of their fauna is little known. Heilprin (1890) reports only one species of gorgonian from the Veracruz reefs and remarks that the vast gorgonian sea gardens so typical of the Bermudas are lacking. The single species that he records, *Plexaura flexuosa*, belongs to the West Indian fauna, and it seems likely that other West Indian species occur there. Heilprin notes further that *Xiphigorgia* (now *Pterogorgia*) *anceps* was found at Progreso, Yucatán, another record indicative of the West Indian fauna. The occurrence of the West Indian reef species *Gorgonia flabellum* on

the Texas coast (one unpublished record in the U. S. National Museum) needs to be verified.

In the deeper waters (10–500 fathoms) of the southeastern Gulf, practically all of the alcyonarians are West Indian species belonging to genera of wide distribution. The Gorgonellidae, Chrysogorgiidae, Primnoidae, and Muriceidae replace in predominance the plexaurids and gorgoniids of very shallow water. Most of the species are widespread throughout the Antilles and probably also in the Caribbean. From the occurrence of such characteristic forms as *Bebryce grandis* and *Scleracis guadalupensis* in the extreme northern Gulf, it is probably safe to assume that a good proportion of the West Indian species are present throughout the Gulf of Mexico wherever bottom conditions permit. There is no evidence as to the composition of the alcyonarian fauna of this bathymetric range in the western part of the Gulf, and intensive collecting should be done in that region to clarify the distribution patterns of the West Indian species as they enter the Gulf of Mexico.

The limited deep-sea dredging which has been done in the Gulf of Mexico has resulted in very few alcyonarian records. The isidid gorgonian, *Acanella eburnea*, which was taken in depths ranging from less than 200 to above 950 fathoms in the Gulf of Mexico, is also known from the northwestern Atlantic, the West Indies and Caribbean, the coast of Brazil, and the eastern Atlantic, always at considerable depths. Beyond the 1,000-fathom contour, three pennatulid species have been dredged: *Umbellula güntheri*, *U. lindahlii*, and *Funiculina quadrangularis*, all of which also occur at extreme depths in the northern and eastern Atlantic.

There seems to be no truly endemic element in the alcyonarian fauna of the Gulf of Mexico. The strictly shallow-water forms of the northern half are also the predominant species along the Carolina-Georgia coast, while those of the southern part are typically West Indian. The species of moderate depths throughout the Gulf are West Indian, and a northern element does not appear to be present. Finally, the characteristically deep-sea forms thus far known from the Gulf are of wide distribution at similar depths throughout the Atlantic and are possibly even cosmopolitan.

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ANTHOZOA: THE ANEMONES

By JOEL W. HEDGPETH, *Scripps Institution of Oceanography, University of California*

There is as yet no systematic study of the anemones of the entire Gulf of Mexico including the Tortugas region. The papers of McMurrich, especially 1889, and Watzl (1922) on Bahamas actinians, together with Duerden's (1902) report on Porto Rican species, are useful aids to the study of the Tortugas anemone fauna which apparently is about the same as that of the Bahamas. For the Gulf of Mexico proper there is only the recent paper by Carlgren and Hedgpeth (1952) on species from Texas and Louisiana. The collections reported in this work indicate a mixture of tropical, West Indian forms and species of the Middle Atlantic coast. Of particular interest is the finding of *Aiptasiomorphia luciae* at Port Aransas, adding yet another locality for that ubiquitous species. The accompanying table, (table 1), compiled principally from the literature, indicates the affinities of the common species found at Bahamas and Tortugas. This is supplemented by brief notes on some of the more interesting forms.

TABLE 1.—*Synopsis and known distribution of anemones in Bahamas, Tortugas, and the Gulf of Mexico*

[Compiled from the literature; synonymy (in parentheses), after Carlgren, 1949]

Species	Woods Hole	Beaufort	Bermuda	Bahamas	West Indies	Gulf of Mexico			Depth	Remarks
						Tortugas (or Keys)	Louisiana	Texas		
Order CORALLIMORPHARIA										
CORALLIMORPHIDAE										
Corynactis bahamensis Watzl				X					Shore	
Ricordea florida Duch. et Mich. (*Heteranthus floridus*)				X	(*)				do	*St. Thomas and Jamaica.
ACTINODISCIDAE										
Paradiscosoma neglecta (Duch. et Mich.)				X	(*)				do	*St. Thomas, Haiti, Jamaica.
Paradiscosoma carlgreni (Watzl) (*Rhodactis carlgreni*)				X					do	
Rhodactis sancti thomae (Duch. et Mich.) (*Actinothrix sancti thomae*)			X	X	(*)				do	*Jamaica.
Order ACTINIARIA; Suborder ENDOCOELANTHEAE										
HALCURIIDAE										
Halcurias pilatus McMurrich						X			100 fathoms	
Suborder NYNANTHEAE										
ALICIIDAE										
Lebrunia danae (Duch. et Mich.) (*L. neglecta*; *Cradactis variabilis*)			X	X	(*)	X			Shore	*Curaçao, St. Thomas, Jamaica.
ACTINIIDAE										
Actinia bermudensis (McMurrich) (*Diplactis bermudensis*)			X	X	(*)					*Curaçao?
Actinia grobbeni Watzl				X						
?Anemonia elegans Verrill			X	X						
Anemonia sargassensis Hargitt	X	X						X	Pelagic, on sargassum.	
Bunodosoma cavernata (Bosc)		X			X		X	X		
Leipsiceras pollens (McMurrich) (*Bolocera pollens*)						X			+100 fathoms	
Anthopleura krebsi (Duch. et Mich.)					(*)			X	Shore	St. Thomas, Jamaica.
Anthopleura varioarmata Watzl				X					do	
Condylactis gigantea (Weiland) (*C. passiflora*)			X	X	X	X				
Bunodactis stelloides (McMurrich) (*Aulactinia stelloides*)			X	X	(*)					Curaçao, Jamaica.

TABLE 1.—*Synopsis and known distribution of anemones in Bahamas, Tortugas, and the Gulf of Mexico*—Continued

Species	Woods Hole	Beaufort	Bermuda	Bahamas	West Indies	Gulf of Mexico			Depth	Remarks
						Tortugas (or Keys)	Louisiana	Texas		
ORDER CORALLIMORPHARIA—Con.										
ACTINIIDAE—Continued										
Phyllactis flosculifera (Le Sueur) (*Asteractis flosculifera; Oulactis fasciculata* McM.)			X	X	(*)					St. Thomas.
Phyllactis conquilegia (Duch. et Mich.) (*Asteractis expansa* Duerden)					X					
MINYADIDAE										
Minyas olivacea (LeSueur)					X		X	X	Pelagic	
STOICHACTIDAE										
Stoichactis helianthus (Ellis) (*Discosoma anemone*)			X	X	X	X				
PHYMANTHIDAE										
Phymanthus crucifer (Le Sueur)			X	X	X					
ACTINOSTOLIDAE										
Paranthus rapiformis (LeSueur) (*Ammophilactis rapiformis*)	New Haven	X					X	X	Shallow water +10 faths. ?	
Subtr. Acontiaria										
ISOPHELLIDAE										
Telmatactis roseni (Watzl) (*Phellia roseni*)				X						
HORMATHIDAE										
Actinauge longicornis Verrill	X	X			X	X			100–250 faths.	
Calliactis tricolor (Le Sueur)		X			X	?		X	Shore–10/20 faths.	
Stephenouge spongicola (Verrill) (*Sagartia spongicola*)	X					X			100 faths.	
AIPTASIIDAE										
Aiptasia pallida (Verrill)		X	?				X	X		
Aiptasia tagetes (Duch. et Mich.)			X	X	(*)					Curaçao, Jamaica.
Bartholomea annulata (Le Sueur) (*Aiptasia annulata; Carlgreniella robusta* Watzl)			X	X	X			X		
Bartholomea werneri Watzl				X						
Heteractis lucida (Duch. et Mich.) (*Aiptasia lucida*)				X	(*)					St. Thomas, Jamaica.
AIPTASIOMORPHIDAE										
Aiptasiomorpha luciae (Verrill) (*Sagartia, Diadumene, luciae*)	X	X						X		
DIADUMENIDAE										
Diadumene leucolena (Verrill) (*Sagartia leucolena*)	X	X						?	Shore	
Order CERIANTHIARIA										
Cerianthiopsis americanus Verrill		X					?		Shallow water to about 10 faths.	
Cerianthromorphe brasiliensis (Carlgren)									10–14 faths.	Brazil, New Mexico

NOTE: The following species, so far known only from the northwestern Gulf of Mexico, have recently been described by Carlgren and Hedgpeth (1952): Andwakiidae, *Andwakia isabellae;* Actiniidae, *Bunodactis texaensis;* Aiptasiomorphidae, *Aiptasiomorpha texaensis;* Sagartiidae?, *Botryon tuberculatus;* Zoantharia, Zoanthidae, *Palythoa texaensis.*

Of all the animals living in the sea the anemones are at the same time among the most beautiful and most difficult to study.. A sound basis for the study of anemones is a detailed series of notes on the living animals including color sketches or photographs, measurements, and descriptions of the nematocysts, and a set of well-prepared slides of various parts of each species. Each marine laboratory or station should compile a set of color photographs, camera lucida drawings of the nematocysts (under oil immersion) making up the cnidom, and serial sections for each species in its fauna. A collection of huddled lumps of coelenterate flesh is almost useless to all but the

most thorough-going specialist in this group, and in the absence of satisfactory material our knowledge of Gulf coast actinians will remain in its present fragmentary state.

NOTES ON COMMON SPECIES

Lubrunia danae **(Duchassaing and Michelotti).**

This anemone is conspicuous for the large, branched outgrowths ("pseudotentacles" or "fronds") at the top of the column just below the tentacles. The animal is brownish and lives in hollows in coral rock. It is common at Tortugas and was described from there by Hargitt (1911) as *Cradactis variabilis*. McClendon (1911), in a paper on habits of several invertebrates, provides a color plate.

Anemonia sargassensis **Hargitt.**

A well characterized anemone both in habit and appearance. Originally described from sargassum drifting into Woods Hole, it is found on that plant as it drifts ashore along the Texas coast and is recorded from Beaufort by Field (1949). It is a small, rather squat, velvet-brown species.[1] The tentacles may be tinted green and are occasionally branched (fig. 60).

Bunodosoma cavernata **(Bosc).**

The common jetty form of the Texas coast, especially at Port Aransas and Port Isabel. Cary (1906) found it common on the Cameron jetties. It was originally described from the Carolina coast and is a characteristic member of the Beaufort fauna. It is a muddy to dull brown colored anemone with pearl gray vesicles on the column, with reddish to brownish or bluish tentacles, but usually with a red stripe on the back of the larger tentacles (fig. 60). Some specimens are entirely cherry red. The West Indian *B. granulifera* is considered to be a synonym of this species (Carlgren 1952).

Anthopleura krebsi **(Duchassaing and Michelotti).**

Previously known from St. Thomas and Jamaica, a colony of small individuals occurs on the Port Isabel jetties. The column and tentacles are white, with rows of bright red verrucae which are larger and more regular toward the top of the column (fig. 60).

[1] M. D. Burkenroad contends (in litteris) that there is another common species on Gulf *Sargassum*, smaller than *Anemonia*, and reproducing commonly by longitudinal fission. Carlgren (in litteris) thinks it possible that this may be a *Bundeopsis*. This problem cannot be clarified until the anemones of the Atlantic Sargassum are critically studied.

Bunodactis texaensis **Carlgren and Hedgpeth.**

A conspicuous gray anemone, superficially resembling *Bunodosoma cavernata*, but with verrucae instead of vesicles on the column and a pattern of darker gray or greenish to light brown splotches on the disc (see color plate, Calgren and Hedgpeth). It occurs on the jetties at Galveston and offshore near Port Aransas.

Minyas olivacea **(LeSueur.)**

A pelagic antillean species which occasionally drifts ashore on the coasts of Texas and Louisiana, sometimes in considerable numbers. The animal is an olive brown color, with the tentacles apparently reduced to knoblike processes. The animal remains at the surface by means of a float in the pedal disc. According to observations of M. D. Burkenroad, *Minyas* will shed its float in an aquarium, but does not produce a new one under these conditions. It may be that the mature *Minyas* (as yet unknown) is a sessile form.

Condylactis gigantea **(Weinland).**

The "passion flower" anemone is common at Tortugas, the Bahamas, Miami, and various places in the West Indies. The color of the column varies from bright scarlet to brownish, the tentacles are brownish or paler than the column and usually tipped with scarlet.

Stoichactis helianthus **(Ellis).**

The "sun flower" anemone is a characteristic West Indian species common in the Bahamas and at Tortugas. It is easily identified by the broad, incompletely retractile disc with its large number of short, stubby tentacles. The disc is greenish or with green patches, and the peristome is usually bright yellow. The tentacles are greenish to yellow.

Paranthus rapiformis **(LeSueur).**

A characteristic member of the shallow water bottom assemblage along the Texas coast. Cary found it washed ashore along the Cameron beach. It is found off Beaufort and along the coast northward to New Haven. Although this species has a moderately well developed basal disc, it is a burrowing form. The column is whitish, the disc green with faint salmon markings (fig. 60). Specimens brought on deck in a trawl or dredge contract to a spherical shape resembling peeled onions.

Calliactis tricolor **(LeSueur).**

Common on the shells of the gastropod *Rehderia* off the southern Atlantic coast and sometimes

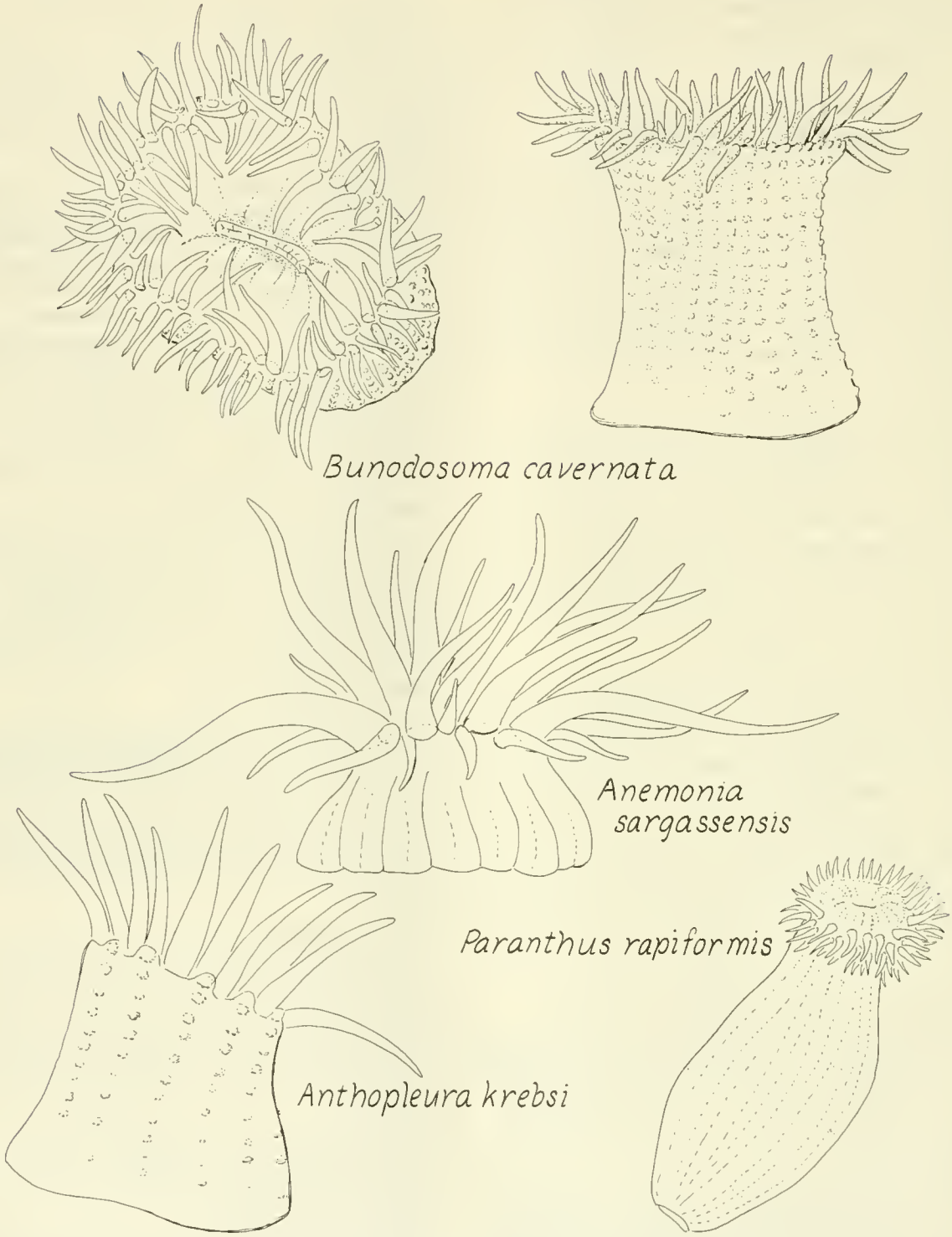

FIGURE 60.—Anemones from the northern coast of the Gulf of Mexico.

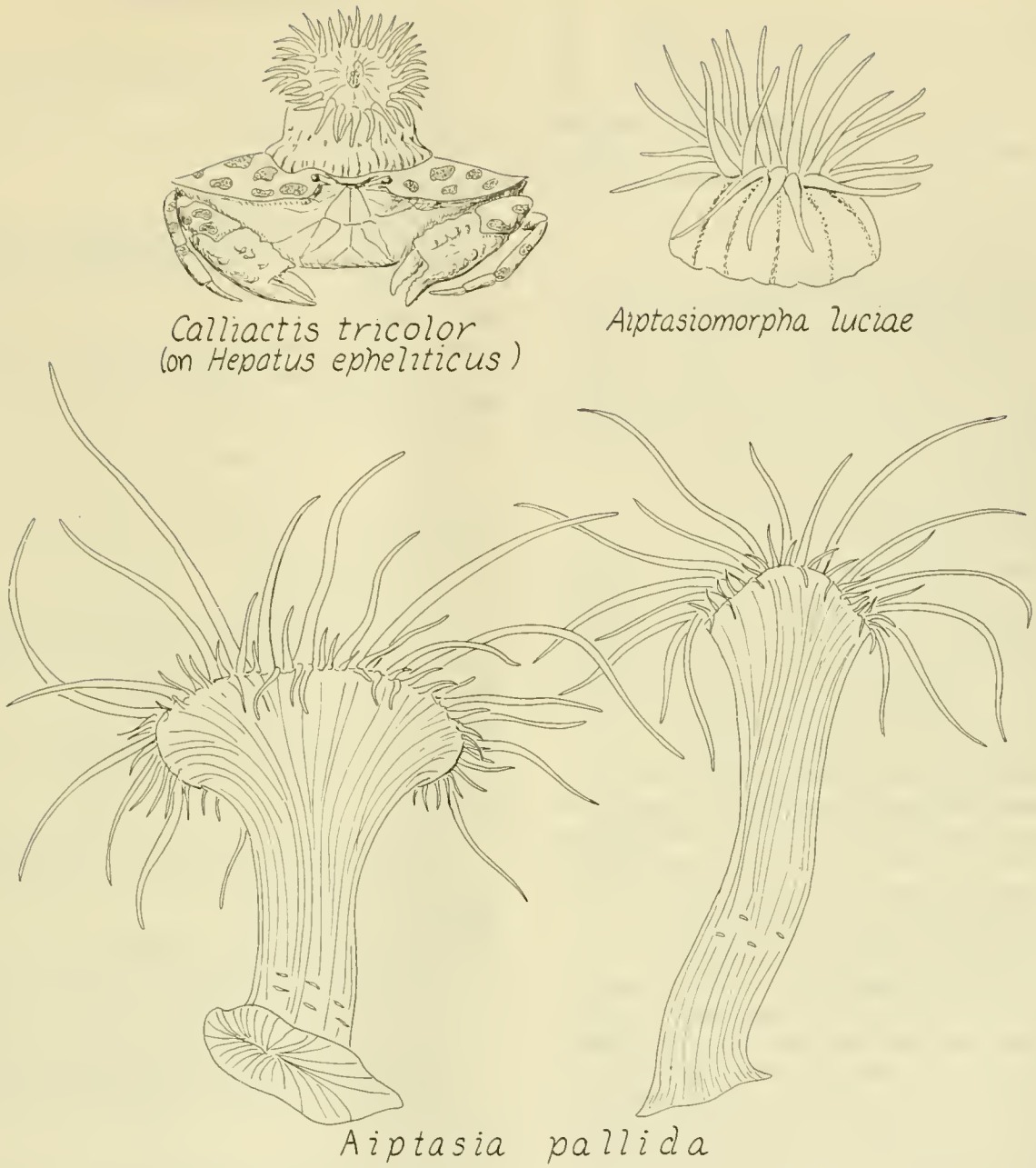

FIGURE 61.—Anemones from the northern coast of the Gulf of Mexico.

abundant on hermit crab shells and oxystome crab carapaces (fig. 61) in comparatively shallow water along the Texas coast. Occasionally, a specimen is found living in shallow water attached to some immobile substrate. The column is whitish, cream colored or brownish with darker vertical stripes and darker brown spots marking the cinclides at the base of the column; the acontia are bright orange; the tentacles are pinkish to red with darker bandings. The directives are often more deeply colored than the other tentacles. This is a common West Indian species.

Aiptasia pallida **(Verrill).**

According to Cary, this species (fig. 61) was common on the jetties at Cameron in 1906; I have not seen it on Texas jetties but found it

commonly on oysters near Port Isabel. It is usually rich brown with darker stripes. The tentacles may be solid brown, or whitish. The brown color is due mainly to zooxanthellae. Offshore, in about 10 fathoms, there is a pale powder blue phase found in old Pinna shells. The species is known from the Carolina coast, especially at Beaufort, where it occurs in large colonies (Carlgren 1952).

***Bartholomea annulata* (LeSueur).**

The tentacles appear to be ringed because of the annular swellings or incomplete bands of nematocyst batteries. The column is whitish at the base, darkening to brown near the top. The tentacles are brown. The species is found in Bermuda, Bahamas, and the West Indies, and a specimen has been collected at Port Isabel, Texas.

***Aiptasiomorpha luciae* (Verrill).**

Easily identifiable by its olive green column with orange vertical stripes (when not in a colorless phase), this little anemone (fig. 60) is almost cosmopolitan. It was first observed by Verrill at Woods Hole but may have spread originally from Japan. It is found on the Pacific coast of North America, at various places in Europe, and now from the Texas coast (Port Aransas).

***Aiptasimorpha texaensis* Carlgren and Hedgpeth.**

A small, salmon pink to whitish species locally common in bays of Texas and Louisiana. It has been recorded from salinities as low as 9 parts per thousand, and seems to be an estuarine species. It is usually found on oysters and piling.

***Cerianthemorphe brasiliensis* Carlgren.**

This cerianthid has been collected near the coast of Texas and northeastern Mexico, and was originally described from San Sebastián, Brazil. Cary reported a colony of cerianthids from the Chandeleur Islands, which may be this species, or possibly *Cerianthiopsis americanus*, which occurs at Beaufort. These large burrowing anemones are difficult to collect, and no specimen from the Chandeleurs has come to notice.

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[Caution: The corrections made by Carlgren (1952) and Carlgren and Hedgpeth (1952) concern only the anemone section.]

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GULF OF MEXICO MADREPORARIA[1]

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By reason of the great difference in their normal habitat corals fall into two very distinct groups. The hermatypic or reef corals are usually, but not always, large and massive or branching in form. They are usually associated with other corals in building considerable masses of living coral reef. The deep-water or ahermatypic corals, on the other hand, are usually small and solitary though sometimes branching in form.

Hermatypic corals grow in water up to 50 fathoms in depth but are only active in reef building in depths to 25 fathoms. Most reef growth occurs in less than 15 fathoms. Ahermatypic corals are found mostly in deeper water from the edge of the continental slope to the neighborhood of 3,000 fathoms. The majority live between 90 and 300 fathoms. The temperature range for reef corals is approximately 19° C. to 36° C. (63° F. to 97° F.) with an average minimum, however, of 22° C. (72° F.). Ahermatypic corals live best within a range from about 8° C. to 21° C. in the West Indian region.

The distribution of reef corals in the Gulf of Mexico and the relation of the coral fauna of this area to those of neighboring areas is dependent upon the physiological requirements of corals. These have been studied in detail and are discussed by Vaughan in a series of papers describing experiments carried out at Dry Tortugas.

The average optimum salinity for reef corals is 36 parts per thousand, although a range of 27 to 40 parts per thousand may be tolerated. Exposure to air is also tolerated to a variable extent. Species with more porous skeletons are considerably more resistant to exposure. Strong light is essential to vigorous growth. This is apparently the result of the zooxanthellae which are normally present in the tissues of reef corals. Corals are carnivorous in habit.

Reef corals do not, as a rule, withstand any great amount of sediment and are accordingly found where vigorous water circulation exists The branching corals grow more readily in comparatively still water than do the massive types. A few species such as *Porites furcata* and *Manicina areolata* may be found on muddy bottoms.

Growth rates of corals at Dry Tortugas have been measured by Vaughan. Non-porous species grew at an average rate of 9.0 mm. in diameter and 5.00 mm. in height per year. Porous species increased at an annual rate of 40 mm. in diameter and 25.0 mm. in height. *Montastrea annularis*, a massive type, showed an annual increment in weight of 54.8 percent, whereas, a branching coral, *Acropora palmata*, increased 194.9 percent in weight per annum. Both specimens were approximately 100 grams at the beginning of the experiment. Growth of corals is greater at higher temperatures. Since temperatures in the Gulf of Mexico are generally close to the lower limit of the range, reef growth is accordingly slower than in the warmer seas. Larvae of species found in the Gulf of Mexico have a planktonic life of between 1 and 3 weeks.

Winter temperatures in the Gulf of Mexico are close to the lower limit for vigorous reef growth. There are therefore no strongly developed reefs except for those of the Dry Tortugas, the Florida Keys, and the Alacran and other reefs of the Campeche Bank. Less vigorous reef development is found at Veracruz and at a few other places within the warmer, more southerly waters of the Gulf (fig. 62).

Scattered coral heads which fail to form true reef structures are found elsewhere in the Gulf of Mexico, particularly off the west coast of Florida. Because of the amount of sediment present, they are rarely found close inshore but usually at some distance from the coast in more than 5 fathoms of water. Scattered heads are also found in deeper water in a line running from south of New Orleans toward the Texas coast and in another line running southward parallel to the Texas coast. Sur-

[1] Contribution No. 106 from the Marine Laboratory, University of Miami.

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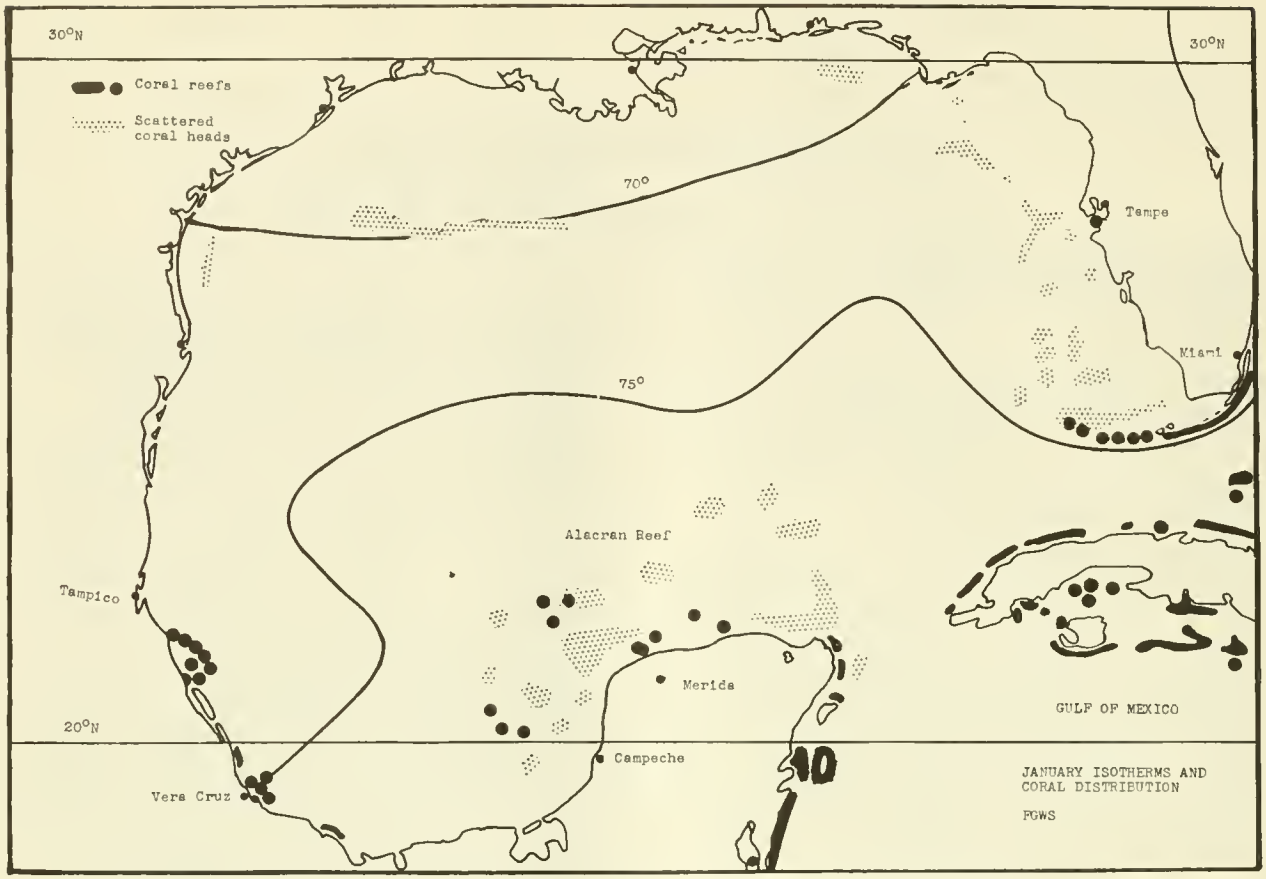

FIG. 62—January isotherms and distribution of corals in the Gulf of Mexico

prisingly few published records exist regarding the presence of reef corals in the Gulf of Mexico. The Alacran reef, described by Agassiz (1878, 1888), the Veracruz reef, described by Heilprin (1890), and the Dry Tortugas and Florida Keys reefs, described by Agassiz (1888), Vaughan, and others complete the list. From these, and various unpublished sources, Joubin (1912) prepared a map of coral reefs of this area. Data concerning patches of scattered coral heads are also shown on the U. S. Hydrographic Office Bottom Sediment Charts 1125 BS and 1126 BS published in 1943. All available records to date are indicated in the accompanying chart which shows approximate locations only.

Except for reefs of the Florida Keys and Veracruz, published accounts of Gulf reefs are insufficient to give an adequate list of species. The fauna is nevertheless typically West Indian. Forty-two of the 51 species known to the West Indies have been recorded from Florida. Only 11 of these are reported from Veracruz (Heilprin 1890).

The Caribbean reef fauna consists of about 26 genera and 51 species (table 1). The species listed here include a number which are undoubtedly varieties or growth forms, such as *Acropora prolifera* and certain species of *Porites*. They are included here, however, since they are recognizably different, and such a list is convenient to field workers who are more concerned with accurate and speedy identification rather than the sometimes debatable questions of taxonomy. For purposes of identification, the handbook of Atlantic reef corals by Smith (1948) is most useful since it contains complete keys and descriptions and is well illustrated. For an authoritative monograph on coral taxonomy, reference should be made to Vaughan and Wells (1943) who provide an extensive bibliography.

TABLE 1.—*Western Atlantic hermatypic species of corals*

[F indicates recorded from Florida; V indicates recorded from Veracruz]

SUBORDER ASTROCOENIIDA	
Family ASTROCOENIIDAE	
1. *Astracoenia pectinata* Pourtalès	F
2. *Stephanocoenia michelini* Edwards and Haime	
SERIATOPORIDAE	
3. *Madracis decactis* (Lyman)	F
ACROPORIDAE	
4. *Acropora cervicornis* (Lamarck)	F
5. *A. palmata* (Lamarck)	FV
6. *A. prolifera* (Lamarck)	FV
SUBORDER FUNGIIDA	
AGARICIIDAE	
7. *Agaricia agaricites* (Linnaeus)	F
8. *A. fragilis* Duna	F
9. *A. nobilis* Verrill	F
SIDERASTREIDAE	
10. *Siderastrea radians* (Pallas)	F
11. *S. siderea* (Ellis and Solander)	FV
12. *S. stellata* Verrill	
PORITIDAE	
13. *Porites astreoides* Lamarck	FV
14. *P. branneri* Rathbun	
15. *P. divaricata* LeSueur	F
16. *P. furcata* Lamarck	FV
17. *P. porites* (Pallas)	F
18. *P. verrilli* Rehberg	
SUBORDER FAVIIDA	
FAVIIDAE	
19. *Favia conferta* Verrill	
20. *F. fragum* (Esper)	F
21. *F. gravida* Verrill	
22. *F. leptophylla* Verrill	
23. *Diploria clivosa* (Ellis and Solander)	F
24. *D. labyrinthiformis* (Linnaeus)	FV
25. *D. strigosa* (Dana)	FV
26. *Colpophyllia amaranthus* (Muller)	F
27. *C. Natans* (Muller)	F
28. *Manicina areolata* (Linnaeus)	F
29. *M. mayori* Wells	F
30. *Cladocora arbuscula* LeSueur	FV
31. *Solenastrea bournoni* Edwards and Haime	F
32. *S. hyades* (Dana)	F
33. *Montastrea annularis* (Ellis and Solander)	FV
34. *M. braziliana* (Verrill)	
35. *M. cavernosa* (Linnaeus)	FV
ASTRANGIIDAE	
36. *Astrangia solitaria* (LeSueur)	F
OCULINIDAE	
37. *Oculina diffusa* Lamarck	FV
38. *O. valenciennesi* Edwards and Haime	
39. *O. varicosa* LeSueur	F
TROCHOSMILIIDAE	
40. *Meandrina meandrites* (Linnaeus)	F
41. *M. brasiliensis* (Edwards and Haime)	F
42. *Dichocoenia stokesii* Edwards and Haime	F
43. *Dendrogyra cylindrus* Ehrenberg	F
MUSSIDAE	
44. *Mussismilia brasiliensis* (Verrill)	
45. *M. hartii* (Verrill)	
46. *Mussa angulosa* (Pallas)	F
47. *Isophyllastrea rigida* (Dana)	F
48. *Mycetaphyllia lamarckana* (Edwards and Haime)	F
49. *Isophyllia sinuosa* (Ellis and Solander)	F
50. *I. multiflora* Verrill	F
SUBORDER CARYOPHYLLIIDA	
CARYOPHYLLIIDAE	
51. *Eusmilia fastigiata* (Pallas)	F

The West Indian fauna includes species belonging to the Astrocoeniidae, Acroporidae, Agariciidae Siderastreidae, Poritidae, Faviidae, Oculinidae, Trochosmiliidae, Mussidae, and Caryophylliidae. None of the Fungiidae are represented and only *Madracis* among the Seriatoporidae. *Montipora*, *Astreopora*, *Goniopora*, and *Trachyphyllia*, all of which exist as fossils of the Caribbean Neogene, are now absent. Genera known only to the West Indian fauna are *Colpophyllia*, *Dendrogyra*, *Meandrina*, *Mussa*, *Mycetophyllia*, *Manicina*, *Isophyllia*, *Isophyllastrea*, *Eusmilia*, *Dichocoenia*, and *Agaricia*. All of the West Indian genera occur on the Florida reefs. Their absence from other parts of the Gulf of Mexico must be ascribed to the existence of unfavorable temperature conditions which permit only the more hardy to live there since their presence on the Florida reefs, their known length of larval life, and the existence of favorable currents are sufficient for dispersal throughout the area.

The ahermatypic corals are much less restricted by geographical boundaries than the hermatypic forms since the required conditions for their existence are widespread throughout the deeper waters of the ocean. The extent of distribution of any species depends partly upon the depth range inasmuch as the deeper the normal habitat, the greater the continuity of suitable environments. On account of the generalized distribution of ahermatypic corals and the lack of adequate surveys of the greater part of the deeper waters of the Gulf of Mexico, it has seemed more useful to provide a list of ahermatypic corals known from the West Indies together with their temperature and depth ranges. It is reasonable to expect that where the proper temperature, depth, and bottom conditions exist in the Gulf, the appropriate West Indian species may be found eventually. Existing accounts of Gulf of Mexico corals are mainly confined to those of Pourtalès dealing with the deep-water fauna of the Florida Keys and between Dry Tortugas and the Campeche Bank.

Descriptions of West Indian ahermatypic species are to be found in Agassiz (1888), Pourtalès (1868, 1871, 1874, 1879, 1880), and Verrill (1883, 1908). A key to Western Atlantic genera is given in Smith (1948). A list of West Indian genera with temperature and depth ranges is given in table 2, compiled from data in Vaughan and Wells (1943).

TABLE 2.—*Ahermatypic genera of corals found in West Indies and Gulf of Mexico with approximate temperature and depth ranges*

SUBORDER ASTROCOENIIDA

SERIATOPORIDAE
Madracis Milne Edwards and Haime
0–800 meters; 10–27° C.

SUBORDER FUNGIIDA

FUNGIIDAE
Fungiacyathus Sars
60–6,000 meters; 1–21° C.

SUBORDER FAVIIDA

ASTRANGIIDAE
Astrangia Milne Edwards and Haime
0–110 meters; 8–28° C.
Phyllangia Milne Edwards and Haime
0–90 meters; 23–28° C.
Colangia Pourtalès
0–580 meters; 6–27° C.

OCULINIDAE
Madrepora Linnaeus
60–1,400 meters; 4–16° C.

TROCHOSMILIIDAE
Dasmosmilia Pourtalès
100–450 meters; 15–22° C.

ANTHEMIPHYLLIIDAE
Anthemiphyllia Pourtalès
170–730 meters; 8–17° C.

SUBORDER CARYOPHYLLIIDA

CARYOPHYLLIIDAE
Caryophyllia Lamarck
0–2,800 meters; 2–27° C.
Coenocyathus Milne Edwards and Haime
0–6,800 meters; 9–26° C.
Cyathoceras Moseley
70–1,100 meters; 3–27° C.
Orysmilia Duchassaing
75–300 meters; 10–20° C.
Bathycyathus Milne Edwards and Haime
55–145 meters; 10–13° C.
Trochocyathus Milne Edwards and Haime
15–1,500 meters; 4–27° C.
Peponocyathus Oravier
100–1,100 meters; 7–21° C.
Tethocyathus Kuhn
65–1,100 meters; 3–12° C.
Deltocyathus Milne Edwards and Haime
15–4,300 meters; 4–28° C.
Ceratotrochus Milne Edwards and Haime
55–700 meters; 5–17° C.
Stephanocyathus Sequenza
360–2,200 meters; 3–12° C.
Turbinolia Lamarck
ss *Batotrochus* Wells
180–570 meters; 11–21° C.
Sphenotrochus Milne Edwards and Haime
22–275 meters; 9–26° C.
Desmophyllum Ehrenberg
35–2,000 meters; 3–23° C.
Parosmilia Milne Edwards and Haime
310–370 meters; 8–12° C.
Coenosmilia Pourtalès
145–450 meters; 13–23° C.
Anomocora Studer
90–820 meters; 4–17° C.
Asterosmilia Duncan
80–200 meters; 13–15° C.

GUYNIIDAE
Guynia Duncan
170–650 meters; 7–12° C.
Stenocyathus Pourtalès
80–820 meters; 7–14° C.
Schizocyathus Pourtalès
100–1,500 meters; 10–18° C.

FLABELLIDAE
Flabellum Lesson
0–3,200 meters; 2–27° C.
Monomyces Ehrenberg
0–1,000 meters; 6–28° C.
Gardineria Vaughan
70–600 meters; 6–18° C.

SUBORDER DENDROPHYLLIIDA

DENDROPHYLLIIDAE
Balanophyllia Wood
0–1,100 meters; 7–28° C.
Dendrophyllia
10–500 meters; 11–27° C.
Tubastrea Lesson
0–400 meters; 15–28° C.
Trochopsammia Pourtalès
500–1,500 meters; 5–7° C.
Enallopsammia Michelotti
270–2,000 meters; 3–15° C.
Thecopsammia Pourtalès
150–1,000 meters; 0–14° C.
Bathypsammia vonMarenzeller
220–330 meters; insufficient data for temperature range.

In shallow water the only ahermatypic corals are 3 or 4 species of *Astrangia*, *Madracis*, and *Phyllangia*. Most species are found in deeper water from the edge of the continental slope downward. A total of 84 species is known. According to Vaughan and Wells (1943), 13 of these are identical with living species of the northern and eastern Atlantic; 59 are endemic. Cosmopolitan species are *Caryophyllia communis*, *Deltocyathus italicus*, *Desmophyllum cristagalli*, *Fungiacyathus symmetricus*, *Lophelia prolifera*, *Madrepora oculata*, and *Stephanocyathus nobilis*.

TABLE 3.—*West Indian fossil genera found living elsewhere.*

SUBORDER ASTROCOENIIDA

ASTROCOENIIDAE
Stylocoeniella Yobe and Sugiyama
Eocene–Oligocene; Recent–Japan, Mauritius
SERIATOPORIDAE
Stylophora Schweigger
Eocene–Miocene; Recent–Red Sea, Indo–Pacific

SUBORDER FUNGIIDA

AGARICIIDAE
Pavona Lamarck
Oligocene–Miocene; Recent–Indo–Pacific
Leptoseris Milne Edwards and Haime
Oligocene–Miocene, Recent–Indo–Pacific
THAMNASTERIDAE
Psammocora Dana
Miocene; Recent–Indo–Pacific
AGATHIPHYLLIIDAE
Diploastrea Matthai
Cretaceous–Oligocene; Recent–Indo–Pacific
PORITIDAE
Goniopora de Blainville
Cretaceous–Miocene; Recent–Indo–Pacific

SUBORDER FAVIIDA

FAVIIDAE
Favites Link
Eocene–Miocene, Recent–Indo–Pacific, Red Sea
Goniastrea Milne Edwards and Haime
Eocene–Oligocene, Recent–Indo–Pacific, Red Sea

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CTENOPHORES IN THE GULF OF MEXICO

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Ctenophores are so fragile that they are not readily preserved or, if they are, certain diagnostic characters may become obscured. Thus, many records of their occurrence are somewhat uncertain. Equally uncertain are their names because about 40 years ago four important papers appeared almost simultaneously (Bigelow 1912; Mayer 1912; Mortensen 1912; Moser 1912), and insofar as I can ascertain, nobody has reviewed the group critically since that time. It is probable, however, that the ctenophore fauna of the Gulf of Mexico is as well known as that of any neighboring area due to Mayer's (1900, 1912) and Fewkes' (1882) observations at the Tortugas. Nevertheless, only about a dozen species have been recorded with any certainty in the Gulf: *Beroë ovata* Bosc; *Bolinopsis vitrea* L. Agassiz; *Cestum veneris* LeSueur; *Eurhamphaea vexilligera* Gegenbaur; *Folio parellela* Fol; *Hormiphora hormiphora* Gegenbaur; *Leucothoe ochracea* [1] Mayer; *Mnemiopsis mccradyi* Mayer; *Ocyropsis crystallina* Rang; *Ocyropsis maculata* Rang; *Tinerfe beehleri* Mayer; *Tinerfe lactea* Mayer (using the names that appear to be acceptable today). This is a slight reduction in the number originally described because a number proved to be identical with species which had been described earlier. This list also includes most of the species that have been reported from neighboring parts of the Atlantic. Whether other species will be found in this area seems problematical. At any rate, although ctenophore species are more numerous in the Gulf, they apparently do not occur in dense swarms as is so characteristic of them in more northern waters.

[1] Fewkes' (1882) record of *Eucharis multicornis* Quoy and Gaimard is considered by Mayer (1912, p. 35) to have been his new species, *Leucothoe ochracea*.

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CHAPTER IX

FREE-LIVING FLATWORMS, NEMERTEANS, NEMATODES, TARDIGRADES, AND CHAETOGNATHS

FREE-LIVING FLATWORMS (TURBELLARIA) OF THE GULF OF MEXICO

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Very little information is available concerning the free-living flatworms of the Gulf of Mexico. Nothing at all has been done with the smaller and microscopic forms so that available material is limited to the polyclads (order Polycladida), and these have been studied only for the Gulf coast of the United States. To the writer's knowledge, no study has ever been made of the turbellarian fauna of the Mexican coast of the Gulf.

The most extensive work on the littoral polyclads of the Gulf of Mexico was done by Pearse (1938) during a stay in the region of Apalachicola Bay near the Alabama border of Florida. This publication, unfortunately, contains some errors. The writer revised Pearse's work in 1940, and the names considered valid are those employed in that article.

The most common littoral polyclads of the Gulf coast, distributed from Florida to Texas, are *Stylochus frontalis* Verrill (=*Sty. inimicus* Palombi, 1931), *Stylochus ellipticus* (Girard) 1850 (=*Eustylochus meridionalis* Pearse, 1938), *Hoploplana inquilina* (Wheeler) 1894, and *Gnesioceros floridana* (Pearse) 1938 (=*Stylochoplana floridana* Pearse, 1938). Illustrations and descriptions of these species will be found in Pearse (1938) and Hyman (1939a, 1940). *Stylochus frontalis* is an oval, gray worm up to 50 mm. in length with nuchal tentacles and a band of eyes around the entire body margin. It lives in association with oysters on which it feeds and to which it may become quite destructive, hence being of some economic importance. The ecology of this polyclad has been treated at some length by Pearse and Wharton (1938). *Stylochus ellipticus* is an oval, gray, olive, cream, or brownish worm with nuchal tentacles and with marginal band of eyes extending only along the anterior part of the body. It, also, is often associated with oysters but is a general littoral species. *Hoploplana inquilina* is a small, oval, rather transparent worm that inhabits the mantle cavity of *Busycon* and *Thais*, possibly other gastropods. Pearse (1938) attempted to separate the form living in *Thais* from that in *Busycon* as a distinct species *thaisana*, but the writer failed to find any good grounds for this distinction and considers *thaisana* to be, at best, a geographical variant. Schechter (1943) found *H. inquilina* living in *Thais floridana* at Barataria Bay, La. *Gnesioceros floridana*, a small, somewhat transparent worm of cuneate form, with nuchal tentacles but without any marginal eyes, is of common occurrence along the Gulf coast. A number of specimens of this species were sent to the writer by Joel W. Hedgpeth who collected them at Port Aransas, Tex., and many were recorded by Pearse from the west coast of Florida. In an Annotated List of the Fauna of the Grand Isle Region 1928–1941, published by the marine laboratory of Grand Isle, La., there is mentioned *Gnesioceros sargassicola lata;* this is presumably a misidentification of *Gnesioceros floridana.*

Other polyclads described by Pearse from the Apalachicola Bay, Fla., region are: *Coronadena mutabilis* (Verrill) 1873 (=*Discocelis grisea* Pearse, 1938); *Latocestus whartoni* (Pearse) 1938 (=*Oculoplana whartoni* Pearse, 1938); *Stylochus oculiferus* (Girard) 1853 (=*Stylochus floridanus* Pearse, 1938); *Zygantroplana angusta* (Verrill) 1893 (=*Stylochoplana angusta* (Verrill) Hyman, 1939); *Euplana gracilis* (Girard) 1850 (=*Conjuguterus parvus* Pearse, 1938); *Enantia pellucida* (Pearse) 1938 (=*Acerotisa pellucida* Pearse, 1938); a species of *Thysanozoon* possibly *brocchi* (Risso) 1818; *Pseudoceros maculosus* Pearse, 1938; *Oligoclado floridanus* Pearse, 1938 (=*Hymania prytherchi* Pearse and Littler, 1938); and *Prosthiostomum lobatum* Pearse, 1938. None of these species have been found in other parts of the Gulf of Mexico except Florida, but some of them extend up the Atlantic coast to the Carolinas. Descriptions and figures of these species are given in the articles by Pearse (1938), Pearse and Littler

(1938), and Hyman (1939, 1940). In addition, there should probably be mentioned *Phaenocelis purpurea* (Schmarda) 1859 (=*Comprostatum insularis* Hyman, 1944), common in the Florida Keys.

There remains to be mentioned the turbellarian fauna of the floating Sargassum. This includes acoels, rhabdocoels, and polyclads and has been discussed by the writer in a previous publication (1939b). There are two common Sargassum polyclads, *Gnesioceros sargassicola* (Mertens) 1833 and *Hoploplana grubei* (Graff) 1892. The former is very similar in appearance to *Gnesioceros floridana*, and there is some suspicion in the writer's mind that the latter may be only a littoral variant of the former. *H. grubei* is a small, oval worm with a white reticulation on a brown ground. Large numbers of both species of polyclads were taken from the Sargassum in the Gulf of Mexico by the Bingham Oceanographic Foundation at Yale University. There are no records of the occurrence of smaller Turbellaria on the Sargassum in the Gulf of Mexico, but presumably some are present there.

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THE NEMERTEAN FAUNA OF THE GULF OF MEXICO

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Nemerteans are found along all the seacoasts of the world and off the shores to depths of hundreds of meters. Some of the species are circumpolar, extending southward along the Atlantic coasts as far as Madeira or South Africa on the east and to southern New England or Florida or the Gulf of Mexico on the west, and in the Pacific to California or Mexico on the east and to Japan on the west. A few species live in both the Northern and Southern Hemispheres and a few others in fresh-water streams and lakes. Some are limited to the polar seas and others to the tropics, but many have a wide geographical range and survive under a great variety of environmental conditions. Some of the bathypelagic species live at depths of 1,000 to 2,000 meters or more, and the populations may be carried for thousands of miles by the deep ocean currents, reproducing generation after generation in their endless circuits throughout the great oceans.

With the exception of the species mentioned in a few local lists of invertebrates, and two papers by Coe (1951, 1951a) no reports of the nemerteans of the Gulf have been published previously. The following account is compiled from the records of the collections sent to the writer from various localities between Apalachicola, Fla., and Port Aransas, Tex., during the past years. No information is yet available for all that portion of the Gulf coast south of the Mexican border, although there are several reports on the species found at various West Indian islands. Several of these species have been found on the Atlantic coast of southern Florida and presumably occur also on the Gulf coast (Coe 1951a).

In the area covered by this report only 17 species are at present known, presumably for the reason that only sporadic efforts have been made toward a complete survey of the littoral fauna of that region. On the Atlantic coast of North America there are 53 known species of nemerteans (Coe 1943) and on the Pacific coast 95 species (Coe 1940). Hence, it seems probable that less than half of all the species now actually living in the Gulf can be included in this report.

Even on the Atlantic coast the nemerteans have been studied extensively only as far south as New Jersey, and our knowledge of the species living between that State and Florida is based on collections made at widely separated localities. It may therefore be assumed that some, perhaps many, additional species remain to be discovered.

GEOGRAPHICAL DISTRIBUTION

All except two of the species known from the northern shores of the Gulf are also found on the Atlantic coast. Therefore, it may be assumed that the nemertean fauna of this part of the Gulf coast is, or has in the geologically recent past been, a continuation of that of the Atlantic coast. It seems quite possible that it is now a separate fauna which was isolated in Pleistocene times by the Florida peninsula. To determine whether the species of the two areas are at present continuous, it is essential to obtain additional collections on both sides of the southern half of that peninsula. It is already known that the species found at Pensacola, on the Gulf side, are similar to those found by the writer personally at St. Augustine, on the Atlantic side. It is also known that these two nemertean faunas are separated by an area in which other species predominate (Coe 1951, 1951a). Because of the great differences in the environmental conditions between the coasts of northern and southern Florida, however, a more or less complete separation would seem probable. In other groups of invertebrates, likewise, the species found in southern Florida are commonly identical with those of the West Indies and northern South America.

The nemerteans evidently represent a conservative group and many of the species have a wide geographical distribution. Of the 17 species at present known from the Gulf of Mexico, all except

Paranemertes biocellata, Amphiporus texanus, and *Cerebratulus ater* are widely distributed on the Atlantic coast, and 4 of them, namely, *Tubulanus pellucidus, Zygeupolia rubens, Zygonemertes virescens,* and *Amphiporus cruentatus* occur also on the Pacific coast but not in Europe; 2 others, *Carcinonemertes carcinophila* and *Tetrastemma vermiculus* are found on European coasts but not in the Pacific; *Oerstedia dorsalis, Tetrastemma candidum,* and *Malacobdella grossa* are circumpolar, inhabiting European shores as well as both the Atlantic and Pacific coasts of North America, while the remaining 5 species, *Carinoma tremaphoros, Lineus socialis, Micrura leidyi, Cerebratulus lacteus,* and *Amphiporus ochraceus* are known only from the Atlantic and Gulf coasts. *Paranemertes biocellata* and *Cerebratulus texanus* have been found only on the northern Gulf coast, while *Cerebratulus ater* is reported from off the Cape of Florida and at Curaçao.

For comparison, it may be noted that 11 of the 53 species found on the Atlantic coast are identical with species in European waters, while 12 of the Atlantic coast species occur also on the Pacific coast, and 2 of these extend also to Japan. No less than 18 of the species found on the Pacific coast are thought to be identical with well-known European species, and others are closely similar (Coe 1943). The nemertean fauna of Bermuda resembles more closely that of Europe and Madeira than that of the American coast in spite of the proximity of the latter.

As a general rule, the invertebrates in the Gulf are much smaller when mature than are the members of the same species in more northern and colder localities. This applies likewise to the nemerteans. To anyone familiar with the species on the New England coast the representatives of the same species in the Gulf appear to be dwarfs. Species living among Bryozoa, algae, and other growths in the intertidal zone farther north are more commonly found beyond the low-tide level in the Gulf.

REPRODUCTION AND REGENERATION

If ripe individuals of both sexes are available, nearly all the species, but especially *Cerebratulus lacteus,* are suitable for the study of embryological development. From a large ripe female of *C. lacteus* many thousand eggs may be obtained, and these usually develop rapidly into pilidium larvae after artificial insemination. Most of the species restore by regeneration the posterior end of the body after injury or removal. *Lineus socialis* provides an example of asexual reproduction by fragmentation and is unexcelled for the study of the complete regeneration of minute fragments of the body. Almost any small piece of the body, provided it contains a portion of one of the nerve cords, will regenerate into a minute replica of the original worm (Coe, 1929–34).

ECOLOGY

Most of the species on the Gulf coast are found burrowing in the sand or mud in the low intertidal zone and below to areas where the depth of water is 10 meters or more. Others live beneath stones or among dead shells, while many of the smaller species occur among Bryozoa, algae, and other growths in the intertidal zone and below.

FOOD

Nemerteans are usually carnivorous, feeding on a great variety of worms, crustaceans, mollusks, and other small, soft-bodied animals. To secure their prey they are furnished with highly specialized sense organs and most of them with a long, eversible proboscis. This organ is a formidable weapon, provided in some species with one or more acutely pointed stylets which puncture and paralyze the prey, allowing the soft parts to be sucked into the mouth. In species without stylets the proboscis, which is covered with a tenacious secretion, can be coiled about the prey, thereby holding it tightly until it can be drawn into the mouth. Only one of the species, *Malacobdella grossa* at present known from the Gulf is commensal living in the mantle cavity of clams. Another species, *Carcinonemertes carcinophila,* sucks the blood in the gills and the substance of the eggs of various species of crabs and is therefore truly parasitic.

KEY TO THE SPECIES AT PRESENT KNOWN FROM THE GULF OF MEXICO

Based Mainly on Easily Recognizable External Characteristics

1. With suction disk at posterior end of body; commensal in bivalve mollusks ..... *Malacobdella grossa*
1. Without suction disk; not commensal in bivalves 2
2. Mouth posterior to brain; proboscis not armed with stylets 3
2. Mouth anterior to brain; proboscis with central stylet and usually with two or more pouches of accessory stylets 9
3. Head without lateral longitudinal grooves 4
3. Head with lateral longitudinal grooves 6
4. Posterior end without slender caudal cirrus 5
4. Posterior end with long caudal cirrus; head acutely pointed ..... *Zygeupolia rubens*
5. Body small, white; posterior end slender ..... *Tubulanus pellucidus*
5. Body when mature usually 30–150 mm. long; red or yellowish red; posterior end broad and flattened ..... *Carinoma tremaphoros*
6. Body slender, rounded; head with two to eight pairs small ocelli ..... *Lineus socialis*
6. Body flattened in intestinal region; head without ocelli 7
7. Lateral margins rounded in intestinal region; not adapted for swimming; color red or rosy ..... *Micrura leidyi*
7. Lateral margins in intestinal region thin; adapted for swimming; color either pale or black 8
8. Color whitish, pale yellow, or rosy ..... *Cerebratulus lacteus*
8. Color black ..... *Cerebratulus ater*
9. Proboscis with central stylet only and no accessory stylets; parasitic on crabs ..... *Carcinonemertes carcinophila*
9. With two or more pouches of accessory stylets; not parasitic 10
10. Proboscis with four or eight pouches of accessory stylets; only one pair of ocelli ..... *Paranemertes biocellata*
10. Proboscis with two pouches of accessory stylets; head with more than one pair of ocelli 11
11. Ocelli numerous, extending posteriorly beyond head ..... *Zygonemertes virescens*
11. Ocelli limited to head 12
12. More than two pairs of ocelli 13
12. Only two pairs of ocelli 15
13. Ocelli in a single row on each side of head; blood corpuscles red ..... *Amphiporus cruentatus*
13. Ocelli in several groups or irregular rows; blood nearly colorless 14
14. Central stylet of proboscis rounded at both ends and slightly constricted in the middle ..... *Amphiporus ochraceus*
14. Central stylet truncated at both ends; not constricted in the middle ..... *Amphiporus texanus*
15. Yellowish, without spots of dark pigment ..... *Tetrastemma candidum*
15. Body small, cylindrical; color variable; irregularly spotted with brown 16
16. Body short and firm; ocelli large, those of the same side not connected by band of pigment ..... *Oerstedia dorsalis*
16. Body soft, yellowish; the two ocelli of same side connected by band of dark pigment ..... *Tetrastemma vermiculus*

SYSTEMATIC DESCRIPTION OF SPECIES

The following pages contain abbreviated descriptions of the species at present known from the Gulf, based mainly on easily recognizable external characteristics. The geographic range, as given, indicates the limits of the species insofar as at present known and should not be interpreted as implying that the species will not later be found elsewhere. Outline drawings of each of the species have been published by Coe (1951a).

Order I PALEONEMERTEA

Family TUBULANIDAE

***Tubulanus pellucidus* Coe, 1940, 1943**

Carinella pellucida Coe, 1895.

The minute worms belonging to this species may be recognized by their slender, white bodies and by the absence of both ocelli and longitudinal grooves on the head. Length when mature 10 to 25 mm., width 1 mm. or less.

The worms live in delicate, cellophane-like tubes among algae and other growths in the intertidal zone and below to a depth of at least 20 meters. Recorded from southern New England to northern Florida, also Pensacola, Fla., and presumably occur elsewhere along the Gulf coast. Found also from Monterey Bay to San Diego, Calif.

Family CARINOMIDAE

***Carinoma tremaphoros* Thompson, 1900; Coe, 1943**

Body pale reddish or yellowish, with broadened posterior end which is without caudal cirrus. Head broad, without ocelli or longitudinal grooves. Length when mature 30 to 150 mm., width 2 to 5 mm. The worms burrow in mud, sandy mud and clay, or live beneath stones in the intertidal zone

and below from Cape Cod to northern Florida and on the Gulf coast at least as far west as Louisiana.

Order 2 HETERONEMERTEA

Family LINEIDAE

Zygeupolia rubens Coe, 1905, 1940, 1943

Valencinia rubens Coe, 1895; *Zygeupolia litoralis* Thompson, 1900.

The worms of this species may be identified by the red or rosy color and sharply pointed head which is devoid of ocelli or longitudinal grooves, as well as by the long caudal cirrus. Length 40 to 80 mm. when mature; width 2 to 5 mm.

Found in sand or beneath stones in the intertidal zone and below from southern New England to northern Florida and on the Gulf coast westward to Copano Bay, Tex.; also from Monterey Bay, Calif., to Mexico.

Lineus socialis Verrill, 1892; Coe, 1943

Nemertes socialis Leidy, 1855.

Recognized by the very slender body with a row of two to eight small ocelli on each side of head and by the tendency of the worms to coil in spiral when disturbed. Length when mature 30 to 150 mm., width 1 to 3 mm. Color variable, often pale olive green, greenish brown, or reddish brown; frontal margin and lateral borders of head whitish; brain region deep red; body sometimes encircled with 6 to 20 or more narrow and inconspciuous rings of lighter color.

Lives beneath stones and among mussels and other growths in the intertidal zone from Bay of Fundy to northern Florida and on the Gulf coast westward to Texas. Locally common and often gregarious.

Differs from all other species on this coast by its capacity for asexual reproduction by fragmentation (Coe 1930). If the body is cut into many small pieces each fragment will ordinarily regenerate into a minute replica of the original worm. For complete regeneration the fragment must contain a portion of one of the nerve cords. This is excellent material for such studies, since the worms or their fragments may live for a year or more in jars of sea water with pebbles in the bottom provided the water is changed occasionally (Coe, 1929–34). A period of asexual reproduction may be followed by dioecious sexual reproduction in which the sexes mate and the eggs are deposited in a thick mucous sheath.

Micrura leidyi Coe, 1943

Meckelia rosea Leidy, 1851; *Cerebratulus leidyi* Verrill, 1892.

One of the most common of the species of ribbon worms in the Gulf and along the east coast of the United States. The body is rather slender, cylindrical in anterior portion, and much flattened in intestinal region; very fragile; head slender, without ocelli; caudal cirrus small; color deep red or purplish red, lighter anteriorly; anterior border of head and mouth region whitish; length 20 to 300 mm., width 1 to 6 mm.

Lives in sand and under stones in the intertidal zone and in shallow water from Massachusetts Bay to the coast of northern Florida and in the Gulf west to Texas. Individuals of this species are among the most fragile of all nemerteans and usually break into many pieces when lifted from the sand. The numerous eggs, which are excellent for embryological studies, are shed into the water from July to October on the coast of southern New England, but the season of reproduction in the Gulf is not at present known. The larvae can be reared to the pilidium stage without difficulty. The adult worms have the capacity for the rapid posterior regeneration of fragments from the anterior part of the body, but if the head is removed it is seldom, if ever, regenerated.

Cerebratulus ater Verrill, 1895; Coe, 1943

Meckelia atra Girard, 1851.

This species is known from a single specimen dredged in deep water off the Cape of Florida, together with two headless fragments which presumably belonged to the same species from near Curaçao. The body is uniformly black in color except for the pale anterior extremity.

Cerebratulus lacteus Verrill, 1892; Coe, 1943

Mecklia lactea Leidy, 1851; *M. ingens* Verrill, 1873.

The body is long and ribbonlike, with flattened intestinal region and thin lateral margins; well adapted for swimming. Ocelli absent; caudal cirrus slender.

Mature individuals are larger than any of the other nemerteans found on the Gulf coast, often exceeding a meter in length. Color variable; whitish, pale yellow, flesh color, pale red or salmon. Young individuals are usually translucent white, with pale yellow or brown intestinal diverticula.

This is a common species, burrowing in the mud or sand in the intertidal zone from Maine to

northern Florida and along the Gulf coast to Port Aransas, Tex.

Each large female produces each season several to many thousand translucent ova which are fertilized in the water and develop rapidly into pilidium larvae. The eggs of this species have been widely used in experimental studies and for class demonstrations. Posterior regeneration takes place readily, but anterior regeneration is limited to the head anterior to the brain, although headless fragments, which can take no food, may live for several months. With occasional changes of the sea water and low temperature, a worm of this species may live for a year or more without food, the body meanwhile being reduced to a small fraction of its original size.

Order 3 HOPLONEMERTEA

Family EMPLECTONEMERTIDAE

Paranemertes biocellata Coe, 1944

This species may be recognized by the slender, pale greenish body with sharply pointed head bearing a single pair of oval, black ocelli near the tip. The proboscis is provided with a slender, cylindrical central stylet and either four or eight pouches of accessory stylets. Size when mature 60 to 120 mm. in length and 2 to 4 mm. in width.

This species is at present known only from Biloxi, Miss., where it has been found burrowing in the intertidal sand flats and in shallow water.

Family CARCINONEMERTIDAE

Carcinonemertes carcinophila Coe, 1902; Humes, 1941, 1942

Nemertes carcinophilon Kölliker, 1845; *Emplectonema carcinophila* Verrill, 1895.

This curious little nemertean is parasitic on the gills of various species of crabs when young and among the egg-masses of the host when mature. The slender body is colored in various shades of red, and there is a single pair of ocelli on the head. The proboscis is very short; it has a slender central stylet but no accessory stylets.

At the time of reproduction a male and a female place their bodies side by side and secrete a thick sheath of mucus in which a hundred or more relatively large eggs are deposited. Development is of the direct type.

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Crabs of the family Portunidae, particularly the lady crab (*Ovipales ocellatus*) and the blue crab (*Callinectes sapidus*) on the American coast and *Carcinus maenas* in European waters are most frequently infested, but representatives of other families are occasional hosts (Humes 1942). With the needlelike central stylet the young worms presumably puncture the gills of the host and suck out the blood, while the adults similarly puncture the eggs of the host and suck out the contents, whether yolk or embryo. It seems probable that additional food for both young and adult is obtained from such small animals as may be encountered.

Found on the Atlantic coast from the Bay of Fundy to Florida and along the Gulf coast to Texas, as well as on European shores from Scotland to the Mediterranean. The typical species reaches a length of 20 to 70 mm., but Humes (1942) found a smaller variety (*C. carcinophila imminuta*) at Grand Isle, La., and at various localities in the West Indies, Panama, and Brazil, which differs in minor morphological details.

Family PROSORHOCHMIDAE

Oerstedia dorsalis Bürger, 1895; Coe, 1940, 1943

Planaria dorsalis Abildgaard, 1806; *Tetrastemma dorsale* Verrill, 1892.

Individuals of this widely distributed species may be recognized by their small, cylindrical, firm bodies often brightly colored and spotted or banded in conformity with their environment. Mature individuals seldom exceed 10 to 20 mm. in length and 1 to 2 mm. in diameter. The head bears four rather conspicuous ocelli. Proboscis relatively large; provided with slender stylet on pear-shaped basis and two pouches of accessory stylets. The colors are extremely variable with shades of red, brown, olive, whitish, or yellowish, spotted, banded or striped with more deeply colored pigment.

Locally abundant among algae, Bryozoa, and other growths on rocks and piles in the low intertidal zone and below on the coasts of Europe to Madeira, on the Atlantic coast of North America from Nova Scotia to northern Florida, on the Gulf coast westward to Texas, and on the Pacific coast from Puget Sound to Mexico. The relatively large eggs undergo the direct method of development.

Family AMPHIPORIDAE

Zygonemertes virescens Montgomery, 1897; Coe, 1940, 1943

Amphiporus virescens Verrill, 1879, 1892; *Ophionemertes agilis* Verrill, 1873; *Amphiporus agilis* Verrill, 1892.

The slender, cylindrical, greenish worms belonging to this species differ from all others known from the region in having very numerous, minute ocelli which extend along the sides of the body far posterior to the brain. Living individuals may also be distinguished from those of other species by their restless, rapid movements. The proboscis sheath extends the entire length of the body, and the proboscis is armed with a slender central stylet with massive basis truncated posteriorly and with two lateral pouches usually containing three accessory stylets each. Length of body when mature 10 to 40 mm., width 1 to 2 mm.

The species is locally common among algae, Bryozoa, and other growths on rocks and other objects in the low intertidal zone and below. It occurs from the Bay of Fundy to northern Florida and along the Gulf coast at least as far as Pensacola, Fla. It is also found on the Pacific coast from British Columbia to Mexico.

Amphiporus cruentatus Verrill, 1879; Coe 1940, 1943

Amphiporus leptacanthus Coe, 1905.

Individuals of this species are easily recognized in life by their pale yellow color with three slender longitudinal red lines representing the longitudinal blood vessels, as well as by the single row of 5 to 10 ocelli on each side of the head. Central stylet of proboscis long and slender on long, slender basis. Length when mature 10 to 30 mm., width 1 to 4 mm. Blood corpuscles bright red.

Lives among algae, Bryozoa, and other growths on rocks and beneath stones and shells in the intertidal zone and below from New England to northern Florida and on the Gulf coast at least as far as Pensacola, Fla., as well as on the Pacific coast from Puget Sound to Mexico.

This is a good species for the study of posterior regeneration, the restoration of a lost proboscis, and the reorganization of fragments cut from the anterior portion of the body.

Amphiporus ochraceus Verrill, 1892; Coe 1943

Cosmocephala ochracea Verrill, 1873; *A. greenmani* Montgomery, 1897.

In this species the body is slender and pale yellow, whitish or grayish in color, sometimes with tinge of orange anteriorly and occasionally with brown intestinal diverticula. The length when mature varies from 10 to 70 mm. and the width 1 to 3 mm. The head bears 6 to 14 small ocelli in irregular rows on each lateral margin, bending medially toward the brain. The proboscis has a slender central stylet and basis, with usually 2 accessory stylets in each of the 2 pouches.

Locally common beneath stones and among algae and other growths in the intertidal zone and below from Massachusetts Bay to Florida and in the Gulf westward to Port Aransas, Tex.

Amphiporus texanus, Coe, 1951, 1951a

This new species represents one of the larger and broader forms of this extensive genus. The type specimen was about 60 mm. in length and 6 mm. in width after preservation. The length of this specimen is therefore only 10 times the greatest width. The head is narrow, about 2 mm. in width, with subterminal mouth and transverse or oblique lateral grooves.

Ocelli.—There are many small ocelli on each side of the head, although the exact number and arrangement could not be determined in this specimen.

Proboscis.—This organ is large and extends nearly the entire length of the body. The central stylet is moderately slender and about two-thirds the length of the relatively massive basis. The latter is nearly rectangular in outline, about four times as long as its diameter, tapering but slightly toward the anterior end and is truncated posteriorly. In this type specimen the basis measured 0.135 mm. in length and from 0.027 to 0.035 mm. in diameter. One of the two accessory pouches contained two well-formed stylets and the other had three which were not yet completed. In this specimen there were 10 rather large proboscidial nerves.

Color.—No record is available regarding the color in life, but the specimen preserved in formalin indicated a pale, reddish brown epidermal pigmentation.

Cerebral sense organs.—These are comparatively larger than in most species of the genus. They are situated lateroventrally and a short distance anterior to the brain.

Geographical distribution.—At present known only from this type specimen which was collected by B. Earp at Port Aransas, Texas.

Family TETRASTEMMATIDAE

***Tetrastemma candidum* McIntosh, 1873, Verrill, 1892; Coe, 1940, 1943**

Fasciola candida Müller, 1774.

These little worms may be identified by the pale green or yellowish green body without markings. Young individuals are pale yellow laterally and green medially. There are two pairs of conspicuous reddish brown ocelli anterior to the brain. The stylet basis is rounded at both ends and slightly enlarged posteriorly. Length of body when mature 10 to 20 mm., occasionally 35 mm.; width 0.5 to 1.5 mm.

Locally common among Bryozoa, algae, and other growths in the intertidal zone and below from Labrador to northern Florida and on the Gulf coast at least as far west as Louisiana. Found also on European coasts, Madeira, and South Africa, as well as on the Pacific coast from Alaska to Mexico. This is a typical circumpolar species.

***Tetrastemma vermiculus* Stimpson, 1857; Verrill, 1892; Coe, 1943**

Polia vermiculus Quatr., 1846.

This species resembles *T. candidum* in many respects but differs in having a light yellow or reddish body variously spotted with brown and in having the two ocelli of the same side connected by a band of dark pigment. Some individuals have paired lateral spots at regular intervals along the entire length of the body.

Locally common among algae and Bryozoa in the intertidal zone and below from the Bay of Fundy to northern Florida and on the Gulf coast westward to Texas. Found also on European coasts from Norway to Madeira.

Order 4 BDELLONEMERTEA

Family MALACOBDELLIDAE

***Malacobdella grossa* (O. F. Müller), 1776**

M. grosa Bürger, 1895; Gering, 1911; Riepen, 1933; Coe, 1940; *M. obesa*, *M. mercenaria* Verrill, 1892.

Body short and broad, wider at posterior end which bears a comparatively large suction disk.

Length when mature 20 to 40 mm., width 8 to 15 mm. Color white, gray, pale yellow, or brownish. Ocelli and cerebral sense organs absent. Alimentary canal narrow, cylindrical, and convoluted; without diverticula. Proboscis slender with weak musculature and without stylets. Gonads in both sexes small and numerous. Eggs that are artificially fertilized develop rapidly without metamorphosis.

Commensal in the mantle cavity of various species of bivalve mollusks; on the Atlantic and Gulf coasts more commonly in *Venus mercenaria* than in any other species. Widely distributed on European shores as far south as the Mediterranean; on the American Atlantic coast from Nova Scotia to Florida, on the Gulf coast westward to Texas, and on the Pacific coast as far south as California. It probably causes little, if any, injury to the host, since it feeds mainly on the larger particles which the clam draws into its mantle cavity but does not ingest.

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ECHINODERIDA OF THE GULF OF MEXICO

By B. G. CHITWOOD, *formerly, Department of Biology, The Catholic University of America*

These are small (0.2–1.0 mm. long) worms presenting a gross similarity to crustaceans, but the body cavity corresponds to a blastocoele. The body is ventrally flattened, covered with a cuticular exoskeleton consisting of 13–14 segments. Segmentation also extends to the musculature and nervous system. The cuticle bears large, segmentally distributed, nonretractile setae and minute spines in scattered or regular arrangement. The mouth is terminal; alimentary canal straight, consisting of mouth, pharynx, esophagus, mid-gut, rectum, and terminal anus. The first segment of the body takes the form of a retractile proboscis armed with hooks and spines. The pharynx has a round lumen, cuticular lining, low cuboidal cellular layer, and external layer of circular muscles; esophagus and mid-gut are simple, nonciliated; small salivary glands are attached to the esophagus.

The body musculature is rather complex, circular muscles being present only in the second zonite. In the remainder of the body the muscles extend from zonite to zonite through the body cavity, usually being attached only at the ends. The nervous system consists of a bilobed dorsal ganglion, paired commissures, and a double ventral nerve trunk with segmentally arranged ganglia. The body cavity is without epithelium. The excretory system consists of a single pair of simple protonephridia opening on the tenth zonite. Gonads are paired, sac-like, with paired sex openings on the thirteenth zonite. Sexes are separate. Specialized copulatory bristles are present in the male. Development includes minor changes in external structure and at least one molt.

These organisms are found in bottom sand feeding on algae or in the slime on crabs and mollusks. Remane (1936) has given a thorough summary of our knowledge of this group.

Systematically, they present an interesting paradox since they show similarities to nematodes, gordiid larvae, gastrotrichs, and Crustacea. They are usually placed with the unsegmented worms (i. e., Subkingdom Scolecida, or Vermes Amera) on the assumption that they are pseudo-segmented. More thorough study of the embryology and post-embryonic development would appear warranted.

Only four species have been reported from North America. These include *Pycnophges frequens*, *Trachydemus mainensis*, and *Echinoderella remanei* reported by Blake (1930) from Maine and *Echinoderella steineri* reported by the writer (1951) from Aransas Bay, Texas.

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FREE-LIVING NEMATODES OF THE GULF OF MEXICO

By B. G. Chitwood and R. W. Timm, *formerly, The Catholic University of America*

NEMATODE ANATOMY

Nematodes are unsegmented, triploblastic pseudocoelomate, dioecious organisms with a complete digestive tract. Externally they are invested with a noncellular cuticle composed of various scleroproteins; cilia are always absent both externally and internally. Immediately beneath the cuticle there is a cellular or syncytial hypodermis concentrated in dorsal, ventral, and paired lateral chords or ridges which project into the body cavity. The musculature of the body wall consists of a single layer of spindle-shaped, uninucleate muscle cells attached throughout their length to the hypodermis between the chords. Since the dorsal and ventral musculature of the body each acts as a unit, movement is whip-like or eel-like. Because of the absence of circular or diagonal muscle layers the squirming movements and transverse contractions seen in turbellarians and annelids are lacking in nematodes. The body cavity is a pseudocoelom containing scattered fixed cells of mesenchymatous origin.

The oral opening is surrounded by lips and sensory papillae or setae. Paired lateral cephalic sensory organs, the amphids, are situated at the labial or post-labial region; they are varied in shape in the different groups of marine nematodes. The mouth cavity or stoma is highly diversified and often there is a relation of stomatal structure to feeding habits. The esophagus is an elongate muscular organ lined with cuticle; it contains three or five esophageal glands the orifices of which may open into the lumen or through teeth into the mouth cavity. Grossly the esophagus may be cylindroid or may consist of several distinct regions and be terminated by a bulb with, or without, a valve. The intestine is a straight tube consisting of a single layer of cells numbering 2 to perhaps 200 in circumference. Various types of intestinal cell inclusions give characteristic appearances to the genera or species. These may be organic or inorganic waste products, stored food materials such as glycogen, oils, and proteins, or absorption products such as plant pigments. Finally, the digestive tract ends in a rectum or cloaca lined with cuticle and opening on the ventral side of the body but never terminally.

The reproductive system consists of one or two tubular gonads. In the female the vulva is ventral, usually near the middle of the body. If paired, the ovaries are opposed and may be either reflexed or outstretched. Most nematodes are oviparous, but viviparous species occur in many families. In the male the testes, if paired, are usually opposed as in the female, but a common duct, the vas deferens, extends from both gonads posteriad to connect with the intestine and form a common cloaca opening ventrally. Specialized copulatory organs in the form of sclerotized spicules are present in the male. A sclerotized guiding piece, the gubernaculum, is almost always present. In addition, the male generally has copulatory sense organs varying according to the different groups.

Various glands empty externally through the cuticle. Of these, the excretory system is the most diversified. In the class Aphasmidea this system consists of a single ventral gland cell in the body cavity emptying through a duct which is usually protoplasmic rather than sclerotized. This is the condition in most aquatic nematodes. In the class Phasmidea the excretory system has a sclerotized terminal duct and one or two lateral canals situated in the lateral chords. Unicellular glands are also connected with the amphids and with similar paired lateral caudal sensory organs, the phasmids. Sublateral paired series of hypodermal glands and three caudal adhesive glands, emptying terminally at the tail, are also usually present in the Aphasmidea.

The most conspicuous element of the nervous system is the circum-esophageal commissure or nerve ring. From it six main nerves run forward and innervate the cephalic sensory organs. Four or more nerves extend posteriad from the nerve ring; of these, one is situated in the dorsal chord, a purely motor nerve; one or more pairs of sensory nerves are situated in the lateral chords; and a single or partially paired nerve is situated in the ventral chord. The latter is the chief nerve of the body, contains ganglion cells, and serves as both a motor and sensory nerve. It may also act as an associational center. Various commissures connect the longitudinal nerves. Somatic sensory organs and genital papillae are served by the lateral nerves and connect with the ventral nerve through the commissures.

A more extensive account of nematode anatomy in general and of the various groups in particular can be obtained from An Introduction to Nematology, by Chitwood and Chitwood (1950). Identification of a large number of marine forms can be had from the lengthy studies of Stekhoven (1935) and W. Schneider (1939).

HISTORICAL RÉSUMÉ

Nematodes of the Gulf of Mexico have received only scant attention. For this reason we have included records of marine nematodes from waters adjoining the Gulf. These total 103 species representing most of the major groups of marine nematodes but probably not over 5 percent of existent forms in the Gulf area. The first report of a nematode from the Gulf was that of *Tricoma major* by Cobb (1912) from Jamaica. Thereafter, Baylis (1915) reported 2 further species from Jamaica, commensals of the land crab, *Gecarcinus ruricola*; Cobb (1920) reported 13 species from Jamaica and 29 species from the Florida coast; Chitwood (1935) reported 3 species from Puerto Rico; Allgén (1947a) reported 15 species from Tobago, British West Indies; and Chitwood (1951) reported 47 species from the Texas coast. All the species reported by Cobb were new, 33 of the 47 species from Texas were new, and 7 of the 15 species from Tobago were new. From these figures it is quite obvious that the nematode fauna of the Gulf of Mexico is quite unexplored. The following checklist is a classified summary of the species reported in the literature.

CLASSIFIED LIST OF SPECIES REPORTED FROM THE GULF OF MEXICO AND ADJACENT WATERS

Class Phasmidea

Phasmids present; caudal and hypodermal glands absent; lateral excretory canals present; terminal excretory duct sclerotized; amphids pore-like.

Order RHABDITIDA

Esophagus in three sections.

Suborder Tylenchina

Stylet present.

Superfamily TYLENCHOIDEA Chitwood and Chitwood, 1937

Dorsal gland orifice near base of stylet.

Family TYLENCHIDAE Filipjev, 1934

Cuticle usually thin, striation moderate to faint; stylet not greatly enlarged; esophageal metacorpus not enlarged.

1. *Halenchus mexicanus* Chitwood, 1951 (fig. 63, A). Locality: Aransas Bay, Tex.

Class Aphasmidea

Phasmids absent; caudal and hypodermal glands usually present; lateral excretory canals absent; terminal excretory duct seldom sclerotized; amphids usually externally modified, pocket-like, circular, spiral, ellipsoid, or vesiculate.

Suborder Enoplina

Stylet absent; cephalic sensory organs usually setose; caudal glands generally present.

Superfamily TRIPYLOIDEA Chitwood, 1937

Cuticle of head not duplicate. Mostly fresh water.

Family IRONIDAE de Man, 1876

Stoma cylindrical.

Subfamily *Ironinae* Micoletzky, 1922

Esophageal gland orifices at stomatal region.

2. *Trissonchulus oceanus* Cobb, 1920. Locality: Miami, Fla.
3. *Trissonchulus reversus* Chitwood, 1951 (fig. 63, F. G). Locality: Aransas Bay, Tex.

Family ENOPLIDAE Baird, 1853

Stomatal region surrounded by esophageal tissue; stomatorhabdions weakly sclerotized; no distinct stomatal capsule.

Subfamily *Leptosomatinae* Micoletzky, 1922

Amphids pocket-like; mandibles absent; esophagus usually cylindrical, rarely conoid; posterior part of esophagus muscular.

4. *Cophonchus ocellatus* Cobb, 1920. Locality: Kingston Harbor, Jamaica.
5. *Anticoma limalis* Bastian, 1865. Locality: Tobago, Br. W. Indies. Reported by: Allgén, 1947. Other localities: Beaufort, N. C., coasts of Holland, Belgium, France, England, Germany.
6. *Paranticoma longicaudata* Chitwood, 1951 (fig. 63, E). Locality: Aransas Bay, Tex.
7. *Leptosomatum bacillatum* (Eberth, 1863) Bastian, 1865. Locality: Tobago, Br. W. Indies. Reported by: Allgén, 1947. Other localities: Mediterranean Sea.

Subfamily *Oxystomininae* (Micoletzky, 1924)

Amphids usually elongate, often internally tuboid; stoma unarmed; esophagus conoid, with weak musculature; cephalic setae usually six, post-cephalic four; preanal supplement absent.

8. *Nemanema simplex* Cobb, 1920. Locality: Port Royal, Jamaica.
9. *Schistodera exilis* Cobb, 1920. Locality: Port Royal, Jamaica.
10. *Porocoma striata* Cobb, 1920. Locality: Biscayne Bay, Fla.

Family ONCHOLAIMIDAE Baylis and Daubney, 1926

Stoma capsuliform, only the posterior surrounded by esophageal tissue; stomatorhabdions heavily sclerotized.

Subfamily *Oncholaiminae* Micoletzky, 1922

Ocelli absent, diffuse pigment spots sometimes present; esophagus cylindrical, not crenate or conoid, vesiculate, or multibulbar; supplements absent or pedunculate.

11. *Anoplostoma heterurum* (Cobb, 1914) Chitwood, 1951. Locality: Ocala, Fla.
12. *Anoplostoma copana* Chitwood, 1951 (fig. 63, C, D). Locality: Copano Bay, Tex.
13. *Pontonema valviferum* Chitwood, 1951. Locality: Rockport, Tex.
14. *Oncholaimus tobagoensis* Allgén, 1947. Locality: Tobago, Br. W. Indies.
15. *Prooncholaimus aransas* Chitwood, 1951. Locality: Aransas Bay, Tex.
16. *Viscosia macramphida* Chitwood, 1951 (fig. 63, B). Locality: Aransas Bay, Tex.
17. *Viscosia papillata* Chitwood, 1951. Locality: Aransas Bay, Tex.
18. *Viscosia glabra* (Bastian, 1865) de Man, 1890. Locality: Tobago, Br. W. Indies. Reported by: Allgén, 1947. Other localities: Coasts of northern Europe and Mediterranean; very widely distributed.

Subfamily *Eurystomininae* (Filipjev 1934)

Ocelli, if present, with pigment and lens. Esophagus conoid to multibulbar, forepart of lumen not notably tuboid; large subventral tooth not remarkably fine; two (rarely 0 or 1) cup-like sclerotized preanal supplements.

19. *Eurystomina americona* Chitwood, 1936. Locality: Rockport, Tex. Reported by: Chitwood, 1951. Other localities: Shackleford's Banks, N. C.
20. *Eurystomina minutisculae* Chitwood, 1951 (fig. 64, E, F). Locality: Aransas Bay, Tex.
21. *Bolbella tobagoense* Allgén, 1947. Locality: Tobago, Br. W. Indies.

Subfamily *Enchelidiinae* (Micoletzky 1924)

Stoma absent in males; stomatal walls distinctly jointed in females; with large needle-like tooth; ocelli, if present, with pigment and lens not closely associated; esophagus conoid to multibulbar with forepart of lumen notably tuboid; well-developed supplements absent.

22. *Enchelidium tenuicolle* Eberth, 1863. Locality: Tobago, Br. W. Indies. Reported by: Allgén, 1947. Other localities: Mediterranean.
23. *Illium exile* Cobb, 1920. Locality: Jamaica.
24. *Catalaimus acuminata* Cobb, 1920. Locality: Biscayne Bay, Fla. Other localities: New Caledonia.

Order CHROMADORIDA

Three part esophagus, commonly with bulb (rarely with pigeon-wing valve), sometimes clavate, very rarely cylindroid; amphids spiral, shepherd's crook, circular, vesiculate, transversely elliptical or very rarely pore-like (*Rhabdolaimus*, *Syringolaimus*); Ovaries outstretched or reflexed.

Suborder CHROMADORINA

Tri-radiate or vertically flattened esophago-intestinal valve, usually very short; stoma, if well-developed, containing a large dorsal tooth, two jaws, three jaws, or six inwardly-acting teeth; 12 stomatal rugae usually present; stoma surrounded by esophageal tissue; preanal supplementary organs usually present; tuboid, papilloid, cup-like, or stirrup-like; ovaries reflexed. Mostly marine, some fresh water forms.

Superfamily CHROMADOROIDEA Stekhoven and de Coninck, 1933

Amphids spiral, circular, or reniform; cuticle striated, usually punctate but not annulate; helmet absent; ambulatory and paired glandular setae absent. Marine and fresh water.

Family CHROMADORIDAE Filipjev, 1917

Amphids rather far forward on head: unispiral, transversely ellipsoid, or kidney-shaped; cuticle coarsely punctate; 12 labial rugae, weakly to moderately developed; stoma surrounded by esophageal tissue, teeth at anterior end; usually internal circle of 6 cephalic papillae and double external circle of 6 papillae and 4 setae; esophageal bulb usually present; esophago-intestinal valve extremely small; cup-like (i. e., chromadoroid) supplements; 2 reflexed ovaries. Marine and fresh water.

Subfamily *Chromadorinae* Micoletzky, 1922

Characters of family.

25. *Rhips ornata* Cobb, 1920. Locality: Ocean Beach, Fla.
26. *Euchromadora striata* (Eberth, 1863) Filipjev, 1917. Locality: Aransas Bay, Tex. Reported by: Chitwood, 1951. Other localities: Atlantic coast of Europe.

27. *Euchromadora vulgaris* (Bastian, 1865) de Man, 1886. Locality: Tobago, Br. W. Indies. Reported by: Allgén, 1947. Other localities: Atlantic coast of Europe.
28. *Paraeuchromadora longicaudata* Chitwood, 1951. Locality: Aransas Bay, Tex.
29. *Actinonema pachydermata* Cobb, 1920. Locality: Key West, Fla.
30. *Spilophorella paradoxa* (de Man, 1888) Filipjev, 1918 (fig. 63, I). Localities: Tobago, Br. W. Indies and Aransas Bay, Tex. Reported by Allgén, 1947; Chitwood, 1951. Other localities: Atlantic coast of Europe and North America.
31. *Chromadora quadralineoides* Chitwood, 1951 (fig. 63, H). Locality: Aransas Bay, Tex.
32. *Chromadorella macrolaimoides* (Steiner, 1915). Locality: Aransas Bay, Tex. Reported by: Chitwood, 1951. Other localities: Sumatra.
33. *Chromadora paramacrolaimoides* Allgén, 1947. Locality: Tobago, Br. W. Indies.
34. *Chromadorella filiformoides* Chitwood, 1951. Locality: Cedar Bayou, Tex.
35. *Chromadorita tentabunda* (de Man, 1880) Filipjev, 1930. Locality: Aransas Bay, Tex. Reported by: Chitwood, 1951. Other localities: Atlantic coast of Europe.
36. *Prochromadorella micoletzkyi* Chitwood, 1951. Locality: Copano Bay, Tex.
37. *Prochromadorella bipapillata* Chitwood, 1951. Locality: Port Bay, Tex.
38. *Spilophora antillensis* Allgén, 1947. Locality: Tobago, Br. W. Indies.
39. *Spilophora mortenseni* Allgén, 1947. Locality: Tobago, Br. W. Indies.

Family MICROLAIMIDAE Stekhoven and de Coninck, 1933

Amphids post-labial, circular to 1–2 spiral; cuticle finely to coarsely punctate; weakly developed labial rugae; stoma cylindroid, surrounded by esophageal tissue, teeth at anterior or mid-stomatal; 6 cephalic papillae and 10 setae or 6 papillae and 4 setae; esophageal bulb usually present; papilloid to chromadoriod supplements; gubernaculum not highly developed; reflexed or outstretched ovaries. Marine and fresh water.

Subfamily *Microlaiminae* Micoletzky, 1922

Cuticle weakly punctate; teeth mid-stomatal; esophagointestinal elongate; papilloid preanal supplements, if present; outstretched ovaries. Marine and brackish.

40. *Microlaimus texianus* Chitwood, 1951. Locality: Aransas Bay, Tex.

Family CYATHOLAIMIDAE Stekhoven and de Coninck, 1933

Amphids multispiral; cuticle coarsely punctate; hypodermal glands often prominent; usually 12 prominent labial rugae; stoma usually cyathiform (i. e., two-part funnel-shaped); teeth, if present, at junction of two parts; esophagus clavate to cylindroid; commonly double gubernaculum, often dentate or denticulate; tuboid, chromadoroid, or setose supplements; reflexed ovaries. Marine.

Subfamily *Cyatholaiminae* Micoletzky, 1922

Stoma funnel-shaped or shallow, without ribs to the base or jaws; dorsal tooth or onchium usually present.

41. *Cyatholaimus sunesoni* Allgén, 1947. Locality: Tobago, Br. W. Indies.
42. *Nannolaimus guttatus* Cobb, 1920. Locality: Biscayne Bay, Fla.
43. *Acanthonchus cobbi* Chitwood, 1951 (fig. 64, B, C). Locality: Rockport Harbor, Tex.
44. *Paracanthonchus truncatus* (Cobb, 1914) Chitwood, 1951. Locality: Silver Springs, Fla. Reported by: Cobb, 1914.

Subfamily *Choanolaiminae* Filipjev, 1934

Stoma deep cyathiform, with 6 or 12 ribs; jaws and dorsal tooth absent.

45. *Halichoanolaimus quatuordecimpapillatus* Chitwood, 1951 (fig. 64, A). Locality: Aransas Bay, Tex.
46. *Synonchium obtusum* Cobb, 1920. Locality: Miami, Fla.

Superfamily DESMODOROIDEA Steiner, 1927

Cephalic capsule or helmet usually present; amphids various, not vesiculate; cuticle annulate, not punctate; glandular tube setae present or absent. Mostly marine.

Family DESMODORIDAE Micoletzky, 1924

Body not epsilonoid; ambulatory bristles and glandular setae absent.

Subfamily *Desmodorinae* Micoletzky, 1924

Amphids circular or spiral; helmet present; cuticle not tiled; dorsal tooth usually present.

47. *Desmodora dubia* Allgén, 1947. Locality: Tobago, Br. W. Indies.
48. *Xennella cephalata* Cobb, 1920. Locality: Key West, Fla.
49. *Ichthyodesmodora chandleri* Chitwood, 1951. Locality: Copano Bay, Tex.
50. *Bolbonema brevicolle* Cobb, 1920. Locality: Kingston Harbor, Jamaica.
51. *Croconema cinctum* Cobb, 1920. Locality: Port Royal, Jamaica.
52. *Leptonemella cincta* Cobb, 1920. Locality: Miami, Fla.
53. *Laxonema majum* Cobb, 1920. Locality: Kingston Harbor, Jamaica.
54. *Stilbonema brevicolle* Cobb, 1920. Locality: Kingston Harbor, Jamaica.

Superfamily DESMOSCOLECOIDEA Stekhoven, 1935

Amphids vesiculate; helmet present; cuticle coarsely striated, without punctations; ocelli common; non-sclerotized stoma; four short cephalic setae; tubular gland setae present; esophagus not clearly divided, glands often free; supplements absent; reflexed ovaries. Marine.

Family DESMOSCOLECIDAE Southern, 1914

Coarsely annulate cuticle, not usually hirsute.

55. *Desmoscolex americanus* Chitwood, 1936. Locality: Aransas Bay, Tex. Reported by Chitwood, 1951. Other localities: Bogue Sound, N. C.

56. *Desmoscolex nudus* Chitwood, 1951 (fig. 64, D). Locality: Rockport, Tex.
57. *Eudesmoscolex luteocola* Chitwood, 1951. Locality: Rockport, Tex.
58. *Tricoma major* Cobb, 1912. Locality: Jamaica.
59. *Tricoma spinosoides* Chitwood, 1951. Locality: Aransas Bay, Tex.
60. *Tricoma filipjevi* Chitwood, 1951. Locality: Aransas Bay, Tex.
61. *Tricoma spinosa* Chitwood, 1936. Locality: Aransas Bay, Tex. Reported by: Chitwood, 1951. Other localities: Bogue Sound, N. C.

Family GREEFFIELLIDAE (Filipjev 1929)

Cuticle not coarsely annulate, usually hirsute.

62. *Greeffiella dasyura* Cobb, 1922. Locality: Biscayne Bay, Fla.

Suborder MONHYSTERINA

Esophago-intestinal valve dorsoventrally flattened, never vertically flattened, usually elongate; stoma, if well-developed, unarmed or without prominent teeth, surrounded or not by esophageal tissue; stomatal rugae absent; papilloid or tuboid supplements, may be minute depressions; outstretched or reflexed ovaries. Marine or fresh water.

Superfamily PLECTOIDEA Chitwood, 1937

Amphids 1–2 spiral or almost circular; punctation, if present, weak; ends of esophageal radii tuboid; reflexed ovaries.

Family LEPTOLAIMIDAE Oerley, 1880

Esophageal bulbar region muscular but without valve; stoma narrow, cylindrical, or presumably absent; cuticle somewhat coarsely striated. Mostly marine.

63. *Leptolaimus plectoides* Chitwood, 1951. Locality: Aransas Bay, Tex.

Subfamily *Rhabdolaiminae* Chitwood, 1951

Ampids pore-like, minute; stoma cylindrical, very narrow. Marine or fresh water.

64. *Syringolaimus smarigdus* Cobb, 1928 (fig. 65, A). Locality: Rockport, Tex. Reported by: Chitwood, 1951. Other localities: Woods Hole, Mass.

Family CAMACOLAIMIDAE Stekhoven and de Coninck, 1933

Amphids basically unispiral; terminal excretory duct never sclerotized; stoma tiny or absent, often armed with dorsal tooth; four cephalic setae; posterior region of esophagus glandular.

Subfamily *Camacolaiminae* Micoletzky, 1924

Amphids anterior to cephalic setae. Marine.

65. *Neurella simplex* Cobb, 1920. Locality: Key West, Fla.
66. *Onchium ocellatum* Cobb, 1920. Localities: Mass. and Key West, Fla.
67. *Onchulella ocellata* Cobb, 1920. Locality: Biscayne Bay, Fla.
68. *Nemella ocellata* Cobb, 1920. Locality: Biscayne Bay, Fla.
69. *Camacolaimus tardus* de Man, 1889. Locality: Aransas Bay, Tex. Reported by: Chitwood, 1951. Other localities: Coasts of Holland.
70. *Digitonchus cylindricaudatus* Chitwood, 1951. Locality: Rockport, Tex.

Subfamily *Aphanolaiminae* Chitwood, 1935

Amphids posterior to cephalic setae. Fresh water or marine.

71. *Alaimella cincta* Cobb, 1920 (fig. 65, B). Localities: Biscayne Bay, Fla., and Aransas Bay, Tex.

Superfamily AXONOLAIMOIDEA Chitwood, 1937

Amphids spiral or variants, rarely circular; cuticle not punctate; stoma, if well-developed, cylindroid to conoid; teeth, if present, as three or six eversible prorhabdions; esophagus three part without valve to clavate; ends of esophageal radii tuboid; outstretched ovaries (reflexed in a few comesomes). Mostly marine.

Family AXONOLAIMIDAE Stekhoven and de Coninck, 1933

Amphids unispiral to shepherd's crook, seldom a broken circle; cuticle usually smooth, punctation absent or minute; supplements papilloid or absent; gubernaculum usually with posterior apophyses; outstretched ovaries.

Subfamily *Axonolaiminae* Micoletzky, 1924

Amphids unispiral, circular to shepherd's crook; stoma conoid with well-developed rhabdions. Marine.

72. *Odontophora angustilaimoides* Chitwood, 1951 (fig. 65, E, F). Locality: Aransas Bay, Tex.

Subfamily *Diplopeltinae* Rauther, 1930

Amphids unispiral, on a sclerotized plaque; stoma weak, walls not sclerotized.

73. *Didelta maculata* Cobb, 1920. Locality: Key West, Fla.
74. *Araeolaimus punctatus* (Cobb, 1920) Chitwood, 1951. Localities: Key West and Biscayne Bay, Fla. Reported by: Cobb, 1920.
75. *Araeolaimus texianus* Chitwood, 1951 (fig. 65, M). Locality: Rockport Harbor, Tex.
76. *Pseudaraeolaimus perplexus* Chitwood, 1951 (fig. 65, L). Locality: Aransas Bay, Tex.

Family COMESOMATIDAE Stekhoven and de Coninck, 1933

Amphids multispiral; cuticle often puctate; stoma cylindroid with three sclerotized points at anterior or reduced; supplements papilloid or absent; gubernaculum with or without posterior apophyses; ovaries usually outstretched. Marine.

77. *Mesonchium poriferum* Cobb, 1920. Locality: Key West, Fla.
78. *Pepsonema pellucidum* Cobb, 1920. Locality: Kingston Harbor, Jamaica.
79. *Laimella longicauda* Cobb, 1920. Localities: Biscayne Bay and Key West, Fla.
80. *Cynura uniformis* Cobb, 1920. Locality: Miami, Fla.

81. *Sabatieria hilarula* de Man, 1922 (fig. 65, G, H). Locality: Aransas Bay, Tex. Reported by: Chitwood, 1951. Other localities: Coasts of Holland, Germany, Norway, France, and North Carolina.

Superfamily MONHYSTEROIDEA Stekhoven and de Coninck, 1933

Amphids circular; stoma very diverse; cephalic setae 4 (?), 6, 10, 12, 16, 18, or more; ends of esophageal radii convergent; esophago-intestinal valve usually spheroid to cylindrical; outstretched ovaries. Marine or fresh water.

Family MONHYSTERIDAE Oerley, 1880

Stoma not styletiform; radial muscles of esophagus diffuse, without cuticular attachment points; esophagus cylindrical, without bulb.

Subfamily *Monhysterinae* Micoletzky, 1922

Cuticle not ridged; stoma not sclerotized, usually conoid; three low lips; papilloid sensory organs of internal circle; usually one anterior outstretched ovary. Marine or fresh water.

82. *Diplolaimella ocellata* Chitwood, 1951. Locality: Aransas Bay, Tex.
83. *Cytolaimium exile* Cobb, 1920. Locality: Biscayne Bay, Fla.
84. *Monhystera parva* Bastian, 1865. Locality: Cedar Bayou, Tex. Reported by: Chitwood, 1951. Other localities: Northern coast of Europe, Mediterranean and Red Seas.
85. *Monhystera socialis* Bütschli, 1874 (fig. 65, C, D). Locality: Cedar Bayou, Tex. Reported by: Chitwood, 1951. Other localities: Northern coast of Europe.
86. *Monhystera tobagoensis* Allgén, 1947. Locality: Tobago, Br. W. Indies.
87. *Theristus bütschlioides* Chitwood, 1951. Locality: Aransas Bay, Tex.
88. *Theristus elaboratus* Chitwood, 1951 (fig. 65, I–K). Locality: Copano Bay, Tex.

Subfamily *Xyalinae* Chitwood, 1951

Cuticle coarsely striated; stoma sometimes sclerotized; cephalic setae 6 plus 12; 6 or 3 (?) lips. Marine.

89. *Xenolaimus striatus* Cobb, 1920. Locality: Biscayne Bay, Fla.

Family LINHOMOEIDAE Filipjev, 1929

Stoma not styletiform; esophageal radial muscles concentered, often with cuticular attachment points; esophagus usually with distinct bulb. Esophago-intestinal valve usually very large; one or two outstretched ovaries. Usually marine.

Subfamily *Linhomoeinae* Filipjev, 1929

Cuticle almost smooth; stoma short with weak to moderate sclerotization. Marine.

90. *Catanema exile* Cobb, 1920. Locality: Port Royal, Jamaica.
91. *Anticyathus tenuicaudatus* Cobb, 1920. Locality: Miami, Fla.
92. *Terschellingia longicaudata* de Man, 1907. Locality. Copano Bay, Tex. Reported by: Chitwood, 1951. Other localities: Northern coast of Europe.
93. *Monhystrium wilsoni* (Baylis, 1915) Cobb, 1920. Locality: Jamaica and Puerto Rico on gills of *Gecarcinus ruricola* and *G. lateralis*. Reported by: Baylis, 1915; Cobb, 1920; and Chitwood, 1935.
94. *Monhystrium transitans* Cobb, 1920. Locality: Jamaica and Puerto Rico, on gills of *Gecarcinus ruricola* and *G. lateralis*. Reported by: Cobb, 1920 and Chitwood, 1935.
95. *Halinema spinosum* Cobb, 1920. Locality: Biscayne Bay, Fla.
96. *Metalinhomoeus setosus* Chitwood, 1951. Locality: Aransas Bay, Tex.
97. *Synonemoides ochra* Chitwood, 1951. Locality: Rockport Harbor, Tex.
98. *Anticyclus exilis* Cobb, 1920. Locality: Bath Tub Springs, Jamaica.
99. *Crystallonema fuscacephalum* Cobb, 1920. Locality: Miami, Fla.
100. *Linhomoella exilis* Cobb, 1920. Locality: Biscayne Bay, Fla.

Subfamily *Sphaerolaiminae* Filipjev, 1924

Stoma cylindrical to globoid, heavily sclerotized.

101. *Tripylium carcinicolum* (Baylis, 1915) Cobb, 1920. Locality: Jamaica, on gills of *Gecarcinus ruricola* and *Cardisoma guanhumi*. Reported by: Baylis, 1915 and Cobb, 1920.
102. *Tripylium carcinicolum* var. *calkinsi* Chitwood, 1935. Locality: Puerto Rico, gills of *Gecarcinus lateralis*.
103. *Halanonchus macrurus* Cobb, 1920 Locality: Biscayne Bay, Fla.

GEOGRAPHIC DISTRIBUTION

Very few of the species thus far described from the Gulf and adjoining areas have been encountered by more than one worker so that discussions of geographic distribution are liable to considerable error. *Spilophorella paradoxa* has been reported from numerous localities on the coast of northern Europe, the North American Atlantic coast from Massachusetts to North Carolina, as well as from Tobago, British West Indies, and Aransas Bay, Texas. *Syringolaimus smarigdus* has been reported from Massachusetts and Texas. Both feed on algae, and it may be that their distribution is governed by the movement of the algae in oceanic currents. *Onchium ocellatum* was reported from Massachusetts and Florida, and *Alaimella cincta* was reported from Florida and Texas. Two species were reported as associates of land crabs in Jamaica and Puerto Rico, though the species of hosts appear to differ in the two localities. Two species were reported from North Carolina and Texas, seven species from Europe and Texas and seven species from Europe and Tobago, British West Indies. A

single species was reported from Sumatra and Texas.

Due to the scarcity of qualified American workers the fauna of the European coasts is far better known than the Gulf fauna, and this probably explains the predominance of European forms among species recorded from more than one locality. Allgén (1947b) reported numerous species from the western coast of North America, and these differ from the eastern fauna, as would be expected.

ECOLOGY AND LIFE HABITS

Most marine nematodes are bottom dwellers or live in association with algae, sponges, colonial hydroids, bryozoa, mollusks, decapods, ascidians, and others. Because of their inability to swim freely for long periods of time, they are never typically planktonic (i. e. holoplanktonic). A few nematodes appear capable of directed movement; monhysterids in particular exhibit a very rapid vibratory motion in which the body may appear as an ellipse with two processes at each end, but the worms cannot sustain these swimming movements for more than several seconds. Most nematodes have a slow serpentine motion which is rather ineffective in locomotion without the aid of a substrate for leverage. In their true habitat, however, locomotion is quite efficient (e. g., oncholaims can move rapidly among filamentous algae). Bottom dwellers are usually confined to a sharply restricted local area.

Many European workers, notably Micoletzky and Stekhoven, have paid considerable attention to ecological considerations, e. g., the association of certain species with certain types of bottoms, the frequency of species in a certain habitat, etc. The largest nematode population is to be found in mud rich in organic debris. Stekhoven has estimated that 500–600 nematodes per cubic centimeter may be found in such a bottom. Saprophagous species, carnivores, and algivorous and diatomivorous species abound here. In highly aerated regions such as breakwaters or surf-beaten rocks there is a rich fauna of algivorous species.

There are numerous references in the literature to the food of nematodes among the genera reported from the Gulf of Mexico. Monhysterids and chromadorids in general feed on algae and diatoms; *Monhystera* and *Euchromadora* feed especially on algae—unicellular and filamentous; and *Theristus* on diatoms. The diatoms may be almost half the diameter of the body. In the anterior of the intestine they are filled with bright green pigment, but when the shells are rejected through the anus they usually contain only a small amount of unabsorbed brownish yellow pigment, proving that the diatoms are actually being utilized as food. Chitwood (1951) presumes that *Paranticoma longicaudata* feeds on algae because of elongate, irregular, greenish masses in the lumen and similarly colored cell inclusions. *Halichoanolaimus* has been reported several times as predatory on other nematodes. The genus *Halenchus* belongs to a group primarily parasites of terrestrial angiosperms, but the species *H. fucicola*, first described by de Man (1892), is a parasite of the brown alga, *Fucus*. Such nematodes have a strictly liquid diet, inserting their hollow oral stylet into plant cells and predigesting the contents to some extent. It would be interesting to ascertain the host plant for *H. mexicanus* described from the Gulf of Mexico (Chitwood 1951).

Herbivorous species may usually be recognized as such by the pigments present either in the intestinal lumen or as cell inclusions. Timm (1951) has reinvestigated such cell inclusions in *Syringolaimus smarigdus* which Cobb (1928) first found associated with the common mud snail, *Nassa obsoleta*. Cobb had reported that *Syringolaimus* was feeding on an encrusting orange alga of the genus *Ralfsia* growing on the shell of the snail, but Timm showed by chemical tests of the cell inclusions and contents of the lumen that this worm feeds rather on the filamentous green alga which forms a thick felt mat on the shell of *Nassa*. The junior author has likewise observed the feeding of *Chromadora quadralineoides* obtained in the living state from Chesapeake Bay off Solomons Island, Maryland. This nematode was found in great abundance in association with the bright red sponge, *Microciona prolifera*. Some worms were apparently feeding off the epidermal substance of the sponge through the action of their three, fine teeth, because bright red, finely divided particles were observed in the intestinal lumen. After 2 months in an unaerated aquarium the sponges had died, but the chromadorids were still thriving on small algae trapped by the coarse skeleton of the sponge.

As a general rule, four molts occur in the development of the parasitic and terrestrial free-living nematodes thus far observed, but there has been no formal study on the life cycle of any of the marine nematodes. Neither has the embryology of any marine nematode been worked out. We have recently observed the first three cleavages of *Euchromadora vulgaris* collected at Woods Hole, Massachusetts. In this species the first two cleavages appear to be equal, while the third cleavage is quite unequal in the derivatives of one of the first two blastomeres. The few published illustrations of nemic embryos in aphasmideans would appear to indicate differences from the established pattern in the Phasmidea. This should be an interesting field of investigation. Most species produce relatively few eggs; 1 or 2 fully formed eggs per uterus is the rule in small forms such as *Monhystera* and *Chromadora*, but some of the larger forms such as *Oncholaimus* may contain up to 20 mature eggs per uterus. The number of eggs is characteristic of the species. Eggs may be deposited in the one cell condition or in various stages of development, and a few viviparous marine nematodes have been reported.

Saline content of the water in which the marine nematodes live must be an important factor in their life, since there is practically no overlapping between marine and fresh-water inhabitants. Attempts to acclimate marine nematodes to fresh water, and vice versa, have been unsuccessful. *Rhabditis marina* has recently been found on decaying seaweed along the beach at Woods Hole, Massachusetts. This form has been cultured with bacteria on nutrient agar made up with either sea water or tap water. Specimens taken from either substrate may be transferred directly to tap water or sea water. Both rhabditids and tylenchids are usually soil or fresh-water inhabitants. Study of their osmotic relations should prove interesting. In the Nematoda, as in the Protozoa and Turbellaria, the excretory system is best developed in fresh-water and soil groups (Phasmidea) and less well developed in the marine groups (Aphasmidea). A study of estuarine forms would probably be very helpful in determining the conditions of transition from a marine to a fresh-water biotope.

On the other hand, the influence of oxygen tension is probably not so important as has been surmised. Chitwood and Chitwood (1938) concluded that *Chromadora quadralineoides* and *Oncholaimium oxyure* var. *domesticum* were highly oxygen loving, since they were found in abundance on an aquarium aerator. However, we have cultured the former species for 2 months and the latter for an entire year in small unaerated aquaria. Probably they are able to help satisfy their oxygen requirements from the green algae on which they feed. Few appear to be adapted to anaerobic life.

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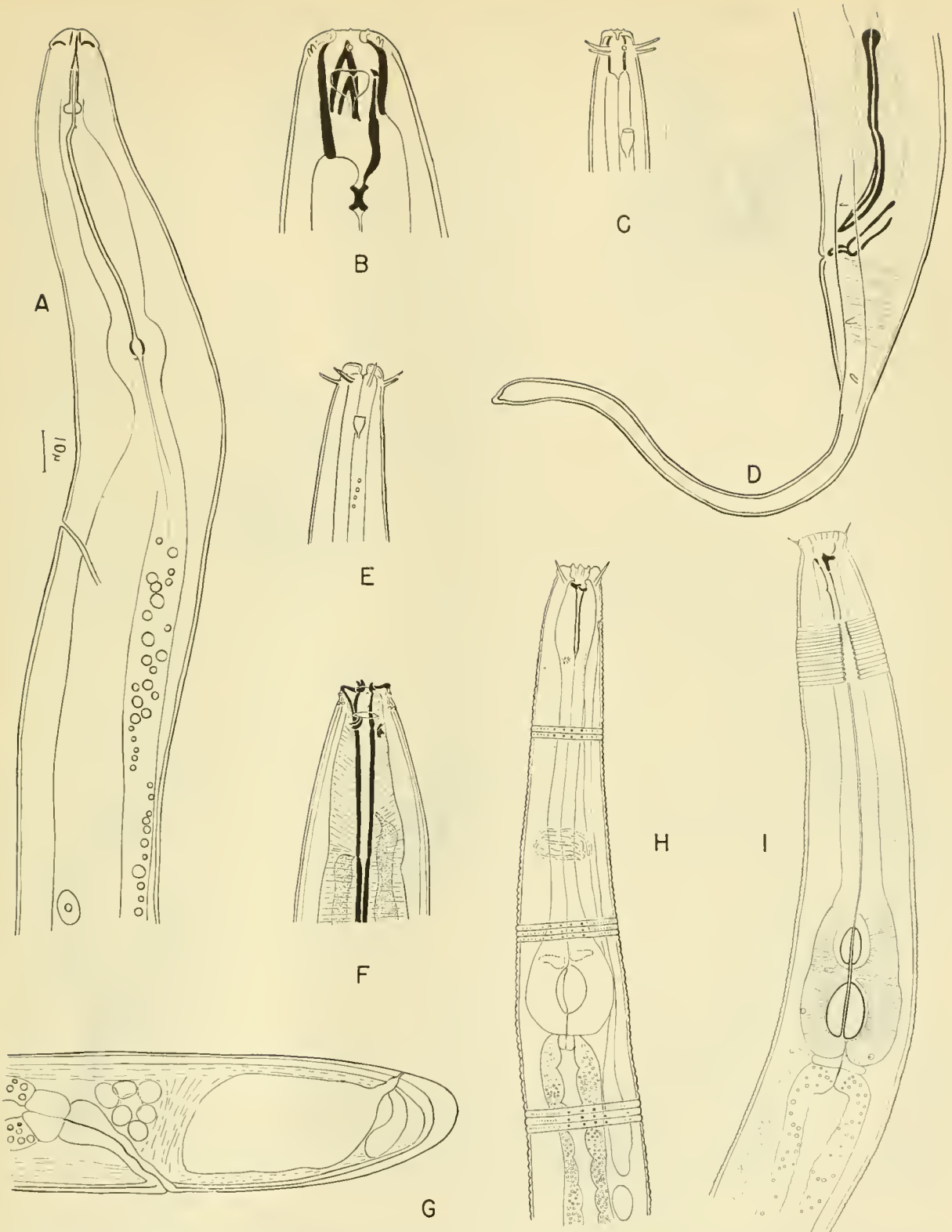

FIGURE 63.—**A.** *Halenchus mexicanus.* Esophageal region. **B.** *Viscosia macramphida.* Head. **C–D.** *Anaplostoma copano.* **C.** Head. **D.** Tail of male. **E.** *Paranticoma longicaudata.* Head. **F–G.** *Trissonchulus reversus.* **F.** Head. **G.** Tail. **H.** *Chromadora quadrelineoides.* Esophageal region. **I.** *Spilophorella paradoxa.* Esophageal region.

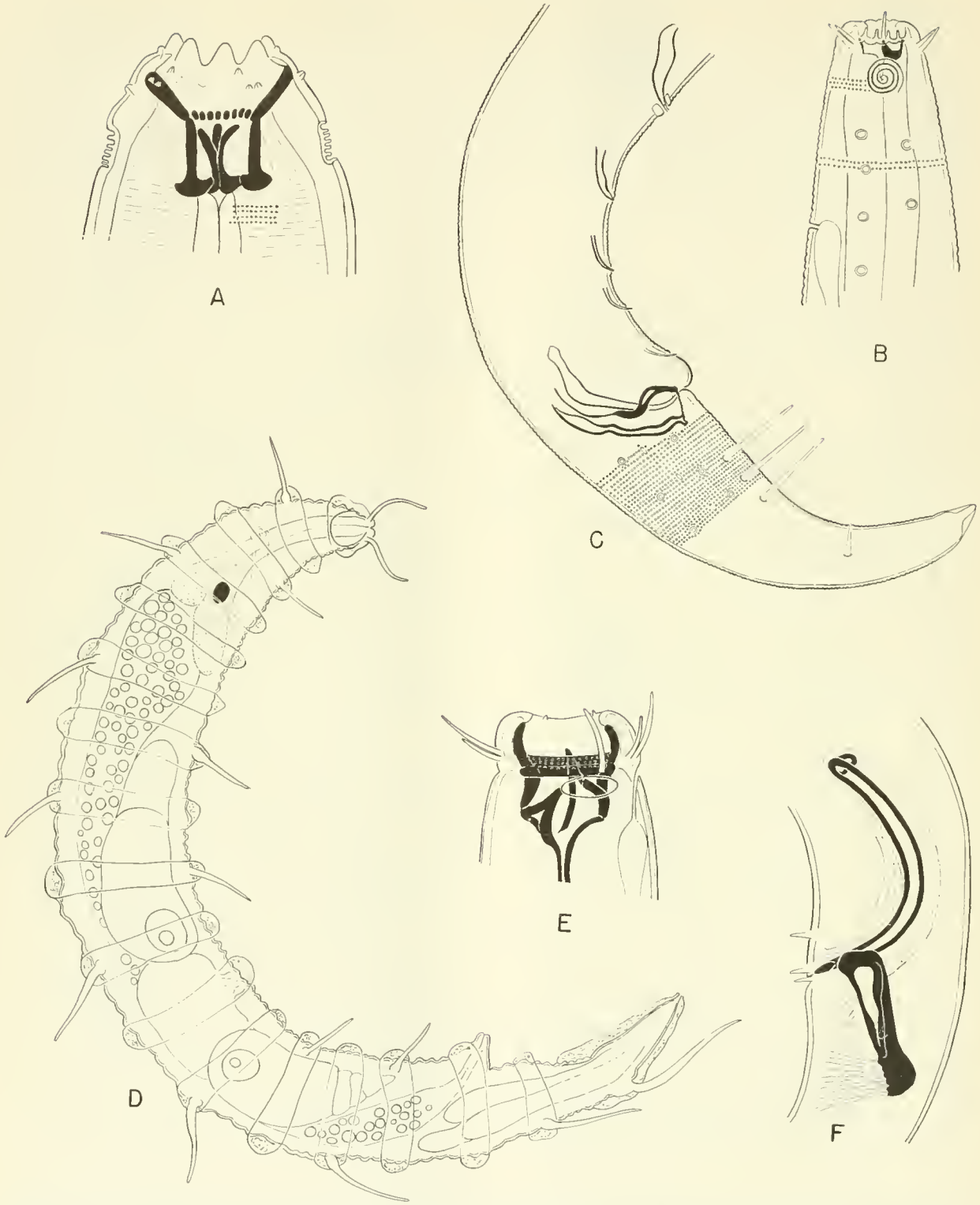

FIGURE 64.—**A.** *Halichoanolaimus quatuordecimpapillatus.* Head. **B–C.** *Acanthonchus cobbi.* **B.** Head. **C.** Male tail. **D.** *Desmoscolex nudus.* **E–F.** *Eurystomina minutisculae.* **E.** Head. **F.** Male cloacal region.

FIGURE 65.—**A.** *Syringolaimus smarigdus.* Esophageal region. **B.** *Alaimella cincta.* Head. **C–D.** *Monhystera socialis.* **C.** Esophageal region. **D.** Male tail. **E–F.** *Odontophora angustilaimoides.* **E.** Head. **F.** Esophageal region. **G–H.** *Sabatieria hilarula.* **G.** Esophageal region. **H.** Spicules and gubernaculum. **I–K.** *Theristus elaboratus.* **I.** Head. **J.** Spicules and gubernaculum. **K.** Tip of tail. **L.** *Pseudaraeolaimus perplexus.* Head. **M.** *Araeolaimus texianus.* Tail of male.

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TARDIGRADES OF THE GULF OF MEXICO

By B. G. Chitwood, *formerly, Department of Biology, The Catholic University of America*

Tardigrades are small, segmented organisms (usually under 1 mm. in length) showing some similarities to arthropods and annelids. They have four pairs of parapodia and a varied number of sensory appendages. The body is covered with a cuticle of uncertain composition; this layer is molted during development. The musculature is apparently smooth, though it presents many similarities to striated muscle. The mesoderm arises as four pairs of gut pockets, and the body cavity is a haemocoele containing a colorless liquid with numerous cells in suspension. A circulatory system is absent. Respiration is through the cuticle. These organisms are very sensitive to lack of oxygen. The nervous system consists of a large, lobed dorsal and lateral ganglion, paired commissures, and a paired ventral nerve with four segmentally paired ganglia.

The digestive tract consists of an ectodermal buccal tube, bulb and esophagus, a mesenteron, and ventral anus. Opening on each side into the buccal tube there is a protrusible stylet. Salivary glands also open into the buccal cavity. The bulb acts as a pump. These forms usually feed on the contents of chlorophyll cells punctured by the stylets; digestion in the mesenteron is intracellular. Posteriorly, there are a group of unicellular to multicellular rectal glands or malpighian tubules at the junction of mesenteron and rectum in the fresh-water forms (Eutardigrada), while such are absent in the marine forms (Heterotardigrada). This is an interesting feature relative to osmoregulation and excretion. We have similar lack of development of rectal glands and lateral excretory canals in the marine nematodes; the protonephridial system of marine Turbellaria is less developed than in fresh-water forms; and the contractile vacuoles of Protozoa are only developed in fresh-water forms.

Sexes are separate, there being a single tuboid gonad suspended dorsal to the intestine. In the male two deferent tubes encircle the intestine to open in a single ventral gonopore anterior to the anus. In the female the single oviduct opens anterior to the anus in the Heterotardigrada and into the rectum in the Eutardigrada. The eggs are usually ornate. Cleavage is total, equal with the formation of a blastula.

Tardigrades usually inhabit algae and mosses. Fresh-water forms are known to be able to resist extensive drying and extremely low temperatures in a state of anabiosis. The two most comprehensive reference articles on the group are those by Marcus (1929) and Cuenot (1932).

The group has been placed with the Acarina, Onychophora, Annelida, and Nematoda. Most of the characters are similar to those of arthropods, but the musculature, digestive tract, and absence of circulatory system present difficulties. For the present, it appears best to place these organisms as a phylum under the Subkingdom Annulosa but to recognize similarities to the Subkingdom Scolecida.

A single species *Bathyechiniscus tetronyx* Steiner, 1926, has been reported from sargassum in the vicinity of Aransas Bay, Texas (Chitwood 1951). This species has also been reported from the South Polar regions (Steiner 1926) and in *Dictyota* washings on the California coast.

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NOTES ON THE CHAETOGNATHA OF THE GULF OF MEXICO

By E. Lowe Pierce, *Department of Biology, University of Florida*

The chaetognaths are elongate, transparent, marine animals. They range in length, when mature, from one-half to several centimeters. One or two pairs of lateral fins and a caudal fin are present. A group of hooks, or seizing jaws, are arranged on either side of the head by means of which they catch their prey. The body is divided into head, trunk, and tail regions. They are hermaphroditic with the ovaries in the trunk and the testes in the tail segment.

Because of their distinctive features the "arrow-worms" are usually set apart from the other worms into a separate phylum. At present about 9 genera and 38 species are recognized. The genus *Sagitta* is by far the largest both in number of species and in number of individuals.

Few published records exist concerning chaetognaths in the Gulf of Mexico. Ritter-Zahony (1910) described specimens taken from the region of the Dry Tortugas, Florida. Conant (1895, 1896) published records of specimens from the West Indies and Beaufort, North Carolina. Davis (1949) and King (1949) briefly mentioned chaetognaths in their studies of plankton of the Gulf coast of Florida. Inasmuch as many of the species in the Gulf have a wide and in some instances an almost cosmopolitan distribution in the warm oceanic waters, many references to such species collected in other bodies of water may be found in the literature.

A recent study (Pierce 1951) of the Chaetognatha of the Gulf coast of Florida revealed two genera and five species present in the inshore waters These are: *Sagitta hispida* Conant, *Sagitta helenae* Ritter-Zahony, *Sagitta tenuis* Conant, *Sagitta enflata* Grassi, and *Krohnitta pacifica* (Aida).

Two samples collected by the *Atlantis* from the offshore waters of the northern portion of the Gulf of Mexico were obtained through the courtesy of the Woods Hole Oceanographic Institution and Dr. H. B. Moore of the Marine Laboratory, University of Miami. The data and the list of species for each sample are given below:

First sample: *Atlantis*. Location: 27°15′ N., 90°09′ W. Date: January 18, 1947. Depth of tow: 495–749 meters.

Species	*Relative abundance*
S. bipunctata Quoy and Gaimard	Common.
S. enflata Grassi	Common.
S. serratodentata Krohn	Common.
S. hexaptera d'Orbigny	Scarce.
S. lyra Krohn	Scarce.
S. macrocephala Fowler	Scarce.
Eukrohnia hamata (Mobius)	Common.
Pterosagitta draco (Krohn)	Scarce.
Krohnitta subtilis (Grassi)	Scarce.

Second sample: *Atlantis*. Location: 26°24′ N., 87°15′ W. Date: 1947.

Note: No further data available from sample.

Species	*Relative abundance*
S. bipunctata	Scarce.
S. enflata	Common.
S. serratodentata	Common.
S. hexaptera	Common.
S. macrocephala	Scarce.
Pterosagitta draco	Common.
Krohnitta subtilis	Common.

A comparison of the chaetognaths taken from the Gulf coast of Florida and the above two samples from the offshore waters in the Gulf reveals an almost totally different fauna. In fact, out of a total of 14 species only 1 (*S. enflata*) was common to both inshore and offshore waters. It would be well to keep in mind. however, that the depth at which the samples were collected was quite different for the first *Atlantis* sample, and probably for the second as well, from that of the coastal samples where the water was never over 20 meters deep. This difference in collecting depth between the two areas would undoubtedly accentuate the faunal differences; however, the appearance of only one species in common is certainly noteworthy.

NOTES ON THE RANGE OF SPECIES COLLECTED IN THE GULF OF MEXICO

S. hispida was collected regularly from the diluted inshore waters along the Gulf coast of Florida. In the Fort Myers and Sarasota region it was not usually taken more than 10 miles offshore. This species has also been collected from the Cedar Keys region, off Cape Sable, the Florida Keys, and 12 miles north of Key West.

Because Conant (1895) failed fully to describe this species which he obtained from Beaufort Harbor, North Carolina, a certain amount of confusion has resulted in later attempts at identification. A comparison of my specimens with the material deposited by Conant in the United States National Museum leaves little doubt about their identity.

S. helenae was a very common species along the Gulf coast of Florida. It was not usually found in the diluted inshore belt of water as was *S. hispida* but was most abundant 5 miles or more offshore where water of approximately normal salinity was encountered.

This species was collected about 40 miles west of Sarasota and probably is to be found much farther offshore in the Gulf. A sample collected by the *Albatross* on March 3, 1885, about 50 miles southeast of the mouth of the Mississippi River contained specimens of *S. helenae*. Ritter-Zahony (1910) obtained it from the Dry Tortugas area and suggests that it is a definitely neritic species.

S. tenuis is also a common form along the west coast of Florida. This small chaetognath, maturing occasionally at 5 millimeters, was taken in water whose salinity varied from 24 to 35 parts per thousand. It was described by Conant in 1896 from specimens obtained in Kingston Harbor, Jamaica. This species was not recognized by Ritter-Zahony (1910) who, not having access to Conant's material in the United States National Museum, failed to consider it a valid species. No references have been found concerning the distribution of *S. tenuis* in the Gulf of Mexico.

S. enflata, by way of contrast, is a true cosmopolitan form and is taken in abundance in the warm waters of all oceans both over the continental shelf and in the open ocean as well. Moreover, it may be collected from the surface to a depth of several hundred meters. Common along the west coast of Florida, in the Florida Current, and in the offshore samples taken by the *Atlantis* in the Gulf, this species is almost certainly very abundant and widely distributed in the Gulf of Mexico.

Little is known about the distribution of *S. bipunctata*, *S. serratodentata*, *S. hexaptera*, *S. lyra*, and *S. macrocephala* in the Gulf of Mexico. Ritter-Zahony (1910) records the first two species from the Dry Tortugas area but apparently did not find the latter three in the collections he examined which, incidentally, were all taken near the surface. These species are all found in the tropic and temperate regions of the Atlantic, Pacific, and Indian Oceans. *S. lyra* and *S. macrocephala* are not typically epiplanktonic forms but are found most abundantly 100 meters or more beneath the surface. As indicated earlier, none of the above were taken in the waters of the west coast of Florida. They are essentially open-water chaetognaths.

Krohnitta pacifica was collected occasionally from the west coast of Florida. It was never very abundant. This species has also been recorded from Australian and Japanese waters. Past errors in its taxonomic status cast some doubt on the extent of its distribution.

Krohnitta subtilis was found in each of the *Atlantis* samples from the Gulf and was never taken close to shore. It is also common to the waters of Australia and Japan.

Eukrohnia hamata was present in one of the *Atlantis* samples. It was never found along the west coast of Florida. This species has been taken in the Atlantic, Indian, and Pacific Oceans.

In order that we may extend our very meager knowledge of the occurrence of the chaetognaths in the Gulf of Mexico added samples are needed from the northern and western portions and especially from the surface and deep waters in the central portion of the Gulf. Studies of such samples will not only add to our information of the distribution of the Chaetognatha but will increase our knowledge of the effects of water movement on the Gulf plankton generally.

SUMMARY

Fourteen valid species of chaetognaths have been collected from the Gulf of Mexico. Five of

these were from the waters of the west coast of Florida. Only one, *S. enflata*, was common to the inshore and offshore samples. The distribution of some of the neritic species are in certain cases well defined and decidedly limited in their offshore range.

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CHAPTER X
PARASITIC WORMS

PARASITIC HELMINTHS

By Asa C. Chandler, *Rice Institute,* and Harold W. Manter, *University of Nebraska*

The helminth parasites of the Gulf of Mexico, with the exception of the trematodes, have been studied very little. The bulk of the collecting done so far has been at the former Biological Laboratory of the Carnegie Institution at Dry Tortugas, Florida, at the eastern side of the Gulf. A few desultory investigations or reports of one or a few species have been made at other points on the United States coast and from the north coast of Cuba, but with the exception of one new species of trematode reported from a manatee no studies have yet been made along the extensive Mexican coast where many new helminths will probably be found, particularly in the nonmigratory fishes of the shallower waters and bays. Practically all the work done so far has been taxonomic and morphological, dealing either with adult or larval forms. Of more than 200 species of trematodes from Gulf animals only 3 life cycles have been studied, and the life cycles of none of the cestodes, acanthocephalans, or nematodes have been studied at all.

The only parasitic helminths of Gulf animals that have thus far been studied comprehensively are the trematodes of oceanic fishes and these only at Dry Tortugas where the pioneer work was done by Linton (1907–10) followed by an extensive study by Manter from 1930–49. Linton also did some pioneer work on the other parasitic helminths of Dry Tortugas, but this work has not been followed up as has the work on the trematodes. It was observed by Linton, however, that Acanthocephala and Nematoda, both in adult and larval stages, are relatively scanty in fishes of Dry Tortugas and in fishes of other southern regions (Bermuda and North Carolina) as compared with their occurrence in fishes at Woods Hole, Massachusetts. Larval cestodes, also, were relatively scanty except adult Tetraphyllidea and Trypanorhyncha in selachians which compared favorably with the numbers found in the Woods Hole, Massachusetts, area.

Chandler (1935a), in a study of 23 species of fish from various parts of Galveston Bay, pointed out a great excess of immature over adult stages of parasites, 15 of 25 of the species identified being larval or immature stages; a scarcity of flukes and adult tapeworms (no elasmobranchs were included in the study); a predominance of Acanthocephala as common adult parasites; and very marked differences in the helminth fauna in local areas, even in the very limited region included in the study. These differences are probably associated with the local distribution of definitive hosts in the case of immature species and of intermediate hosts in the case of adult species. Of 10 species of adults and 15 of immature species, 9 of the former and 11 of the latter were previously undescribed species. This is in contrast to the findings of Manter in oceanic species of fish from Dry Tortugas and suggests, as remarked above, that many new species of fish helminths will be found when the parasites of nonmigratory species of the shores and bays of the western and southern sides of the Gulf are studied.

In preliminary studies on marine fishes from Corpus Christi Bay, Tex., Aaron Seamster (1950) reported in a personal communication that of 30 fish examined, belonging to 16 species, parasites were found in 27. The heaviest load was in the yellow-tail, *Bairdiella chrysura.* However, only 1 specimen, *Menticirrhus americanus,* was infested with an acanthocephalan, *Illiosentis furcatus,* and only 1 specimen, *Synodus foetens,* with a nematode. A few cestode infections were reported.

In addition to the trematodes, cestodes, acanthocephalans, and nematodes considered in the following sections a few other parasitic or semiparasitic helminths have been reported from the Gulf. Several polyclad turbellarians are associated with particular marine organisms on which they are predatory in a semi-parasitic fashion. *Stylochus frontalis* is common in Gulf

oysters. Other species are *Stylochus ellipticus* commonly attacking barnacles, and *Hoploplana inquilina*, attacking the oyster drill (*Thais floridana*). *Hoploplana inquilina* was studied at Barataria Bay, Louisiana, by Schechter (1943), and the others were reported from Apalachicola Bay, Florida, by Pearse and Wharton (1938).

Another helminth recorded from the Gulf is a nemertean, *Carcinonemertes carcinophila* (Kolliker 1845) Coe, 1902, a variety of which, *C. c. imminuta*, was found living on the egg masses of *Callinectes sapidus*, blue crab, at Grand Isle, Louisiana.

NOTE.—Bibliography follows chapter on Nematoda, p. 358.

TREMATODA OF THE GULF OF MEXICO

By HAROLD W. MANTER, *University of Nebraska*

Trematodes of the Gulf of Mexico have been studied chiefly at the former Biological Laboratory of the Carnegie Institution at Dry Tortugas, Florida. The rich fauna there of fishes, mollusks, and Crustacea would suggest a great variety and abundance of these parasites, and such has been proved to be the case. Early in the history of the Laboratory, Linton (1910) and Pratt (1910–16) described species of trematodes from Tortugas. Linton's work in particular indicated the unusual variety of trematode species occurring within fishes there. Later, Miller (1925–29) studied larval stages (cercariae) of trematodes from mollusks; McCoy (1929, 1930) studied the life cycles of two species; and the author (Manter, 1930–49) made extensive taxonomic studies of his collections at Tortugas during 1930–32. As a result, the trematodes of fishes, both surface water species and species down to a depth of about 500 fathoms, are relatively well known. Little study has been made of these parasites elsewhere in the Gulf. Vigueras (1935, 1940) has reported a few species from Cuba; while Chandler (1935), Von Wicklen (1946), and Read (1947) described several species from Galveston Bay. Faust and Tang (1936) described one species from Biloxi Bay, Mississippi.

I am indebted to Dr. Luis R. Rivas for checking and correcting the scientific names of the fish hosts and also for suggestions for the common names of these fishes.

MONOGENEA

The following species of Monogenea have been reported from the gills of fishes at Key West or Tortugas:

1. *Cyclocotyla neomaenis* (MacCallum, 1917) Price, 1943.
   Host: *Lutjanus analis*, Gray snapper.
   Reported by MacCallum (1917).

2. *Cyclocotyla hysteroncha* Fujii, 1944.
   Hosts: *Bathystoma striatum; Brachygenys chrysargyreus; Haemulon flavolineatum*, French grunt.
   Reported by Fujii (1944).

3. *Hexastoma macracanthum* Fujii, 1944.
   Host: *Euthynnus alletteratus*, Little tuna.
   Reported by Fujii (1944).

4. *Heterocotyle floridana* (Pratt, 1910) Price, 1938.
   Host: *Aetobatus freminvillii*, Stingaree.
   Reported by Pratt (1910).

5. *Udonella caligorum* Johnston, 1835.
   Host: On a copepod on gills of *Lutjanus griseus*, Gray snapper.
   Reported by Linton (1910).

6. *Protomicrocotyle mirabile* (MacCallum, 1918) Johnston and Tiegs, 1922.
   Host: *Caranx latus*, Horse-eye jack.
   New record. MacCallum described the species from *Caranx hippos*, Jack crevalle, from the New York Aquarium.

The following four species have been reported from other parts of the Gulf region:

7. *Capsala paeyi* (Vigueras, 1935) Price, 1938.
   Host: Skin of *Makaira ampla*, Blue marlin, from Havana, Cuba.
   Reported by Vigueras (1935).

8. *Encotyllabe monticelli* Vigueras, 1940.
   Host: *Calamus bajonado*, Jolt-head porgy, from north coast of Cuba.
   Reported by Vigueras (1940).

9. *Entobdella squamula* (Heath, 1902) Johnston, 1929.
   Host: Undetermined fish "presumably from Gulf of Mexico."
   Reported by Price (1939).

10. *Neoheterobothrium affine* (Linton, 1898) Price, 1939.
    Host: *Paralichthys* sp., Flounder, from Grand Isle, La.
    Reported by Melugin (1940). This species is known from two species of *Paralichthys* at Woods Hole, Mass.

This small number of species of Monogenea reported does not mean they are uncommon parasites, but rather that they have not been collected and studied. I have a number of species still incompletely studied collected from fishes at Tortugas. Most of them are undescribed species.

ASPIDOGASTREA

1. *Lobatostoma ringens* (Linton, 1907) Eckmann, 1932.
   Hosts: *Calamus calamus*, Saucer-eye porgy; *Calamus bajonado*, Jolt-head porgy.
   Reported by Linton (1910).

2. *Stichocotyle cristata* Faust and Tang, 1936.
   Host: *Rhinoptera bonasus*, Cow-nosed ray from Biloxi Bay, Miss.
   Reported by Faust and Tang (1936).

A large aspidogastrid, *Lophotaspis vallei*, occurs in the loggerhead turtle, *Caretta caretta*. It will be discussed with the trematodes of turtles.

DIGENEA

Approximately 200 species of digenetic trematodes are known from fishes of the Gulf of Mexico, mostly from its eastern region. Linton (1910) reported 53 species from fishes at Tortugas. All except one of these were also collected by the author. Manter (1947, 1949) lists 190 species of digenetic trematodes, including 1 species of aspidogastrid, from the fishes at Tortugas. This number is relatively large compared with the number known from marine fishes of New England, Great Britain, or the Mediterranean, although Yamaguti has reported a larger number from Japanese fishes. The richness of the trematode fauna of the Gulf of Mexico is associated with the great variety of fishes, mollusks, and Crustacea in that region. These four groups are ecologically associated in that trematodes require a molluscan host for their larvae and frequently use Crustacea as second intermediate hosts. Thus, trematode parasites constitute a very common and widespread element in the ecological picture of a region such as Tortugas.

Apparently only 13 other records of trematodes from Gulf of Mexico fishes have been published (Chandler, 1935, 1941; Melugin, 1940; Vigueras, 1940, 1940a, 1940b; Von Wicklen, 1946; Read, 1947). Of these species, four are known at Tortugas. In the list following, the record is from Tortugas or Key West unless otherwise noted.

GASTEROSTOMATA

Family BUCEPHALIDAE

1. *Bucephalopsis longicirrus* Nagaty, 1937; synonym: *Bucephalopsis arcuatus* (Linton, 1900) Eckmann, 1932. New synonymy. Also known from Red Sea.
   Host: *Sphyraena barracuda*, Barracuda.

2. *Bucephalopsis "bennetti"* Melugin, 1940.
   Host: *Paralichthys lethostigma*, Flounder.
   Reported by Melugin (1940) from Grand Isle, Louisiana. The name "bennetti" was printed in this abstract by Melugin, but the trematode was not described, hence the name is a *nomen nudum*.

3. *Bucephalopsis longoviferus* Manter, 1940.
   Host: *Sphyraena barracuda*, Barracuda.

4. *Bucephalus kathetostomae* (Manter, 1934) Manter, 1940.
   Host: *Kathetostoma albigutta*, Stargazer.

5. *Bucephalus priacanthi* Manter, 1940.
   Host: *Priacanthus arenatus*, Glass-eyed snapper.

6. *Bucephalus scorpacnae* Manter, 1940.
   Host: *Scorpaena plumieri*, Scorpion fish.

7. *Bucephalus varicus* Manter, 1940.
   Hosts: *Caranx bartholomaei*, Yellow jack; *C. latus*, jack; *C. ruber*, Runner.

8. *Dollfustrema gravidum* Manter, 1940.
   Host: *Gymnothorax moringa*, Moray.

9. *Prosorhynchus atlanticus* Manter, 1940.
   Hosts: *Mycteroperca microlepis*, Gag; *Mycteroperca venosa*, Yellow-fin grouper.

10. *Prosorhynchus ozakii* Manter, 1934.
    Host: *Epinephelus niveatus*, Snowy grouper.

11. *Prosorhynchus promicropsi* (Linton, 1905) Eckmann, 1932. Host: *Promicrops itaiara*, Jewfish.

12. *Rhipidocotyle angusticolle* Chandler, 1941.
    Host: *Sarda sarda*, Bonito.
    Reported from the Texas coast near Freeport by Chandler (1941).

13. *Rhipidocotyle adbaculum* Manter, 1940.
    Host: *Scomberomorus regalis*, Cero.

14. *Rhipidocotyle baculum* (Linton, 1905) Eckmann, 1932.

15. *Rhipidocotyle barracudae* Manter, 1940.
    Host: *Sphyraena barracuda*, Barracuda.

16. *Rhipidocotyle longleyi* Manter, 1934.
    Host: *Synagrops bellus*.

17. *Rhipidocotyle nagatyi* Manter, 1940.
    Host: *Euthynnus alletteratus*, Little tuna.

18. *Rhipidocotyle transversale* Chandler, 1935.
    Host: *Menidia menidia*, Silverside.
    Reported from Galveston Bay, Texas, by Chandler (1935).

PROSOSTOMATA

Family PARAMPHISTOMATIDAE

19. *Cleptodiscus reticulatus* Linton, 1910.
    Host: *Pomacanthus arcuatus*, Black angelfish.

20. *Macrorchitrema havanensis* Vigueras, 1940.
Host: *Holacanthus tricolor*, Rock beauty.
Reported from north coast of Cuba by Vigueras (1940).

Family PRONOCEPHALIDAE

21. *Pleurogonius candibulus* (Linton, 1910) Ruiz, 1946.
Hosts: *Angelichthys ciliaris*, Queen angelfish; *Pomacanthus arcuatus*, Black angelfish.

22. *Barisomum erubescens* Linton, 1910.
Hosts: *Angelichthys ciliaris*, Queen angelfish; *A. isabelita*, Angelfish; *Pomacanthus arcuatus*, Black angelfish; *Scarus croicensis*, Parrotfish.

Family MEGASOLENIDAE

23. *Hapladena varia* Linton, 1910.
Hosts: *Acanthus coeruleus*, Blue tang; *A. hepatus*, Doctorfish.

24. *Hapladena ovalis* (Linton, 1910) Manter, 1947.
Hosts: *Sparisoma pachycephalum*, Parrotfish; *Pseudoscarus coelestinus*, Parrotfish.

25. *Hapladena leptotelea* Manter, 1947.
Host: *Pomacanthus arcuatus*, Black angelfish.

26. *Megasolena estrix* Linton, 1910.
Hosts: *Kyphosus incisor*, Yellow chub; *K. sectatrix*, Bermuda chub.

Family OPISTHOLEBETIDAE

27. *Opistholebes adcotylophorus* Manter, 1947.
Host: *Diodon holocanthus*, Balloonfish.

Family LEPOCREADIIDAE

28. *Lepocreadium trulla* (Linton, 1907) Linton, 1910.
Host: *Ocyurus chrysurus*, Yellowtail.

29. *Lepocreadium bimarinum* Manter, 1940.
Host: *Lachnolaimus maximus*, Hogfish.

30. *Pseudocreadium anandrum* Manter, 1947.
Host: *Calamus calamus*, Saucer-eye porgy.

31. *Dermadena lactophrysi* Manter, 1946.
Hosts: *Lactophrys tricornis*, Cowfish; *L. trigonus*, Trunkfish; *L. triqueter*, Trunkfish.

32. *Opechona gracilis* (Linton, 1910) Manter, 1947.
Host: *Harengula clupeola*, Pilchard.

33. *Apocreadium balistis* Manter, 1947.
Host: *Balistes vetula*, Queen triggerfish.

34. *Homalometron elongatum* Manter, 1947.
Host: *Gerres cinereum*, Broad shad.

35. *Crassicutis marina* Manter, 1947.
Hosts: *Eucinostomus lefroyi*, Mojarra; *Gerres cinereus*, Broad shad.

36. *Postporus epinepheli* (Manter, 1947) Manter, 1949.
Host: *Epinephelus morio*, Red grouper.

37. *Postporus mycteropercae* (Manter, 1947) Manter, 1949.
Host: *Mycteroperca venenosa*, Yellow-fin grouper.

38. *Lepidapedon levenseni* (Linton, 1907) Manter, 1947.
Host: *Epinephelus morio*, Red grouper.

39. *Lepidapedon elongatum* (Bebour, 1908) Nicoll, 1915.
Hosts: *Coelorhynchus carminatus*, Grenadier; *Epigonus occidentalis; Laemonema barbatulum; Urophycis chesteri.*

40. *Lepidapedon lebouri* Manter, 1934.
Host: Unidentified *Macrouridae.*

41. *Lepidapedon nicolli* Manter, 1934.
Host: *Epinephelus niveatus*, Snowy grouper.

42. *Lepidapedon rachion* (Cobbold, 1858) Stafford, 1904.
Host: *Coelorhynchus carminatus*, Grenadier.

43. *Myzoxenus lachnolaimi* Manter, 1947.
Host: *Lachnolaimus maximus*, Hogfish.

44. *Myzoxenus vitellosus* Manter, 1934.
Hosts: *Calamus calamus*, Saucer-eye porgy; *Decodon puellaris*, Cuban hogfish.

45. *Bianium plicitum* (Linton, 1928) Stunkard, 1931.
Hosts: *Sphoeroides spengleri*, Southern puffer; *Sphoeroides* sp., Puffer; *Monacanthus hispidus*, Filefish.

46. *Multitestis chaetodoni* Manter, 1947.
Hosts: *Chaetodon ocellatus*, Butterfly fish; *C. capistratus*, Butterfly fish.

47. *Rhagorchis odhneri* Manter, 1931.
Hosts: *Alutera schoepfii*, Orange filefish; *Monacanthus ciliatus*, Fringed filefish.

48. *Enenterum aureum* Linton, 1910.
Hosts: *Kyphosus sectatrix*, Bermuda chub; *K. incisor*, Yellow chub.

49. *Cadenatella americana* Manter, 1949.
Host: *Kyphosus incisor*, Yellow chub.

Family OPECOELIDAE

50. *Opegaster synodi* Manter, 1947.
Host: *Synodus foetens*, Lizardfish.

51. *Opecoeloides brachyteleus* Manter, 1947.
Host: *Upeneus martinicus*, Yellow goatfish.

52. *Opecoeloides elongatus* Manter, 1947.
Host: *Upeneus maculatus*, Red goatfish.

53. *Opecoeloides polyfimbriatus* Read, 1947.
Host: *Synodus foetens*, Lizardfish.
Reported from Galveston Bay, Texas, by Read (1947).

54. *Opecoeloides polynemi* Von Wicklen, 1946.
Host: *Polynemus octonemus*, Thread-fin fish.
Reported from Galveston Bay by Von Wicklen (1946).

55. *Pseudopecoeloides gracilis* Manter, 1947.
Host: *Trachurops crumenophthalma*, Goggle-eye jack.

56. *Pseudopecoeloides equesi* Manter, 1947.
Hosts: *Eques lanceolatus*, Ribbonfish; *E. acuminatus*, Ribbonfish.

57. *Pseudopecoeloides carangis* (Yamaguti, 1938) Yamaguti, 1940.
Hosts: *Caranx bartholomaei*, Yellow jack; *C. ruber*, Runner.

58. *Pseudopecoelus priacanthi* (MacCallum, 1921) Manter, 1947.
Hosts: *Priacanthus arenatus*, Glass-eye snapper; *P. cruentatus*, Big-eye.

59. *Pseudopecoelus tortugae* von Wicklen, 1946.
Host: *Coelorhynchus carminatus*, Grenadier.

60. *Pseudopecoelus vulgaris* (Manter, 1947) von Wicklen, 1946.
Hosts: 16 species of fishes collected from depths of 50 to 315 fathoms (see Manter, 1934, p. 293).

61. *Neopecoelus scorpaenae* Manter, 1947.
Hosts: *Scorpaena grandicornis*, Scorpion fish; *S. brasiliensis*.

62. *Neopecoelus holocentri* Manter, 1947.
Host: *Holocentrus coruscus*, Squirrelfish.

63. *Genitocotyle atlantica* Manter, 1947.
Hosts: *Carapus affinis*, Pearlfish; *Haemulon flavolineatum*, French grunt; *Malacoctenus macropus*, Blenny; *Opisthognathus* sp., Jawfish; *Syngnathus robertsi*, Pipefish.

64. *Opecoelina helicoleni* Manter, 1934.
Host: *Helicolenus maderensis*.

65. *Opecoelina scorpaenae* Manter, 1934.
Host: *Scorpaena cristulata*, Scorpion fish.

Subfamily *Plagioporinae*

66. *Plagioporus crassigulus* (Linton, 1910) Price, 1934.
Hosts: *Calamus bajonada*, Jolt-head porgy; *C. calamus*, Saucer-eye porgy; *Decodon puellaris*, Cuban hogfish; *Diplodus holbrookii*, Spot-tail pinfish.

67. *Hamacreadium consuetum* Linton, 1910.
Host: *Haemulon plumieri*, White grunt.

68. *Hamacreadium gulella* Linton, 1910.
Hosts: *Lutjanus analis*, Muttonfish; *L. griseus*, Gray snapper.

69. *Hamacreadium mutabile* Linton, 1910.
Hosts: *Lutjanus analis*, Muttonfish; *L. apodus*, Schoolmaster; *L. griseus*, Gray snapper; *L. jocu*, Dog snapper; *L. synagris*, Lane snapper; *Anisotremus virginicus*, Porkfish; *Ocyurus chrysurus*, Yellowtail.

70. *Hamacreadium oscitans* Linton, 1910.
Hosts: *Anisotremus virginicus*, Porkfish; *Brachygenys chrysargyreus*, Bronze grunt; *Haemulon carbonarium*, Caesar grunt; *H. plumieri*, White grunt; *H. sciurus*, Yellow grunt.

71. *Helicometra execta* Linton, 1910.
Hosts: *Doratonotus megalepis*; *Eques acuminatus*, Ribbonfish; *Haemulon plumieri*, White grunt; *H. sciurus*, Yellow grunt; *Halichoeres bivittatus*, Slippery dick; *H. poeyi; H. radiatus; Labrisomus bucciferus; L. haitensis; Lachnolaimus maximus*, Hogfish; *Mycteroperca venenosa*, Yellow-fin grouper; *Thalassoma bifasciatum*, Slippery dick.

72. *Helicometra fasciata* (Rud., 1819) Odhner, 1902.
Hosts: *Prionotus alatus*, Sea robin; *Prionodes* sp.; *Bellator militaris*.

73. *Helicometra torta* Linton, 1910.
Hosts: *Epinephelus morio*, Red grouper; *E. striatus*, Nassau grouper.

74. *Stenopera equilata* Manter, 1933.
Host: *Holocentrus ascensionis*, Squirrelfish.

75. *Helicometrina nimia* Linton, 1910.
Hosts: 14 species of fishes including cardinal fish, porgies, snappers, and scorpion fishes.

76. *Helicometrina parva* Manter, 1933.
Host: *Halichoeres bivittatus*, Slippery dick.

77. *Podocotyle pearsei* Manter, 1934.
Host: *Urophycis chesteri*.

78. *Eurycreadium vitellosum* Manter, 1934.
Host: *Laemonema barbatulum*.

Subfamily *Horatrematinae*

79. *Horatrema crassum* Manter, 1947.
Hosts: *Odontoscion dentex*, Corvina; *Eques acuminatus*, Ribbonfish; *E. lanceolatus*, Ribbonfish; *Haemulon carbonarium*, Caeser grunt.

Subfamily *Notoporinae*

80. *Neonotoporus yamagutii* Manter, 1947.
Host: *Trachurops crumenophthalmus*, Goggle-eye.

Family ACANTHOCOLPIDAE

81. *Monorchistephanostomum gracile* Vigueras, 1942.
Host: *Sphyraena barracuda*, Barracuda.
Reported from north coast of Cuba by Vigueras (1942).

82. *Stephanostomum* sp.
Host: *Galeichthys felis*, Sea catfish.
Recorded by Melugin (1940) from Grand Isle, La.

83. *Stephanostomum casum* (Linton, 1910) MacFarlane, 1936.
Hosts: *Ocyurus chrysurus*, Yellowtail; *Lutjanus analis*, Muttonfish; *Lutjanus griseus*, Gray snapper.

84. *Stephanostomum lineatum* Manter, 1934.
Hosts: *Lacmonema barbatulum; Phycis cirratus; Urophycis regius.*

85. *Stephanostomum microstephanum* Manter, 1934.
Host: *Epinephelus niveatus*, Snowy grouper.

86. *Stephanostomum megacephalum* Manter, 1940.
Host: *Caranx latus*, Horse-eye jack.

87. *Stephanostomum promicropsi* Manter, 1947.
Host: *Promicrops itaiara*, Jewfish.

88. *Stephanostomum sentum* (Linton, 1910) Manter, 1947.
Hosts: *Calamus bajonado*, Jolt-head porgy; *C. calamus*, Saucer-eye porgy; *Haemulon sciurus*, Yellow grunt; *H. plumieri*, White grunt.

89. *Stephanostomum coryphaenae* Manter, 1947.
Host: *Coryphaena hippurus*, Dolphin.

90. *Stephanostomum dentatum* (Linton, 1900) Manter, 1931.
Hosts: *Epinephelus adscencionis*, Rock hind; *E. morio*, Red grouper; *Mycteroperca venenosa*, Yellow-fin grouper.

91. *Stephanostomum ditrematis* (Yamaguti, 1939) Manter, 1947.
Hosts: *Caranx latus*, Horse-eye jack; *C. ruber*, Runner.

Family ZOOGONIDAE

92. *Steganoderma parexocoeti* Manter, 1947.
Host: *Parexocoetus mesogaster*, Flying fish.

93. *Steganoderma hemiramphi* Manter, 1947.
Host: *Hemiramphus brasiliensis*, Halfbeak.

94. *Steganoderma elongatum* Manter, 1947.
Host: *Strongylura timucu*, Houndfish.

95. *Diphterostomum americanum* Manter, 1947.
Host: *Brachygenys chrysargyreus*, Bronze grunt.

96. *Dcretrema fusillum* Linton, 1910.
Hosts: *Abudefduf saxatilis*, Sergeant major; *Decodon puellaris; Ocyurus chyrsurus*, Yellowtail; *Priacanthus arenatus*, Big-eye; *Upeneus parvus*, Goatfish.

97. *Diplangus paxillus* Linton, 1910.
Hosts: *Anistoremus virginicus*, Porkfish; *Balistes vetula*, Queen triggerfish; *Brachygenys chrysargyreus*, Bronze grunt; *Haemulon flavolineatum*, French grunt; *H. plumieri*, White grunt; *H. sciurus*, Yellow grunt; *H. macrostomum*, Gray grunt.

98. *Diplangus parvus* Manter, 1947.
Hosts: *Haemulon flavolineatum*, French grunt; *H. carbonarium*, Caesar grunt.

99. *Diplangus miolecithus* Manter, 1947.
Hosts: *Haemulon album*, Margate fish; *H. parra*, Sailor's choice.

100. *Brachyenteron parexocoeti* Manter, 1947.
Host: *Parexocoetus mesogaster*, Flying fish.

101. *Brachyenteron peristedioni* Manter, 1934.
Host: *Peristedion platycephalum.*

Family FELLODISTOMATIDAE

102. *Pycnadena lata* (Linton, 1910) Linton, 1911.
Host: *Calamus calamus*, Saucer-eye porgy.

103. *Pycnadenoides calami* Manter, 1947.
Host: *Calamus bajonado*, Jolt-head porgy.

104. *Baccigcr harengulae* Yamaguti, 1938.
Host: *Harengula clupcola*, Pilchard.

105. *Antorchis urna* (Linton, 1910) Linton, 1911.
Hosts: *Angelichthys ciliaris*, Queen angelfish; *A. isobelita*, Angelfish; *Pomacanthus arcuatus*, Black angelfish.

106. *Megalomyzon robustus* Manter, 1947.
Host: *Lachnolaimus maximus*, Hogfish.

107. *Proctoeces erythraeus* Odhner, 1911.
Hosts: *Calamus bajonado*, Jolt-head porgy; *C. calamus*, Saucer-eye porgy.

108. *Mesolecitha linearis* Linton, 1910.
Host: *Acanthurus caeruleus*, Blue tang.

109. *Tergestia laticollis* (Rud., 1819) Odhner, 1911.
Hosts: *Auxis thazard*, Frigate mackerel; *Euthynnus alletteratus*, Little tuna.

110. *Tergestia pectinata* (Linton, 1905) Manter, 1940.
Hosts: *Trachurops crumenophthalmus*, Goggle-eye; *Priacanthus arcuatus*, Big-eye.

111. *Tergestia acuta* Manter, 1947.
Host: *Caranx bartholomaei*, Yellow jack.

112. *Benthotrema plenum* Manter, 1943.
Host: Unidentified Lizard fish.

113. *Lissoloma brotulae* Manter, 1934.
Host: *Brotula barbata.*

114. *Lomasoma gracilis* (Manter, 1934) Manter, 1935.
Host: *Peristedion miniatum.*

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115. *Lomasoma monolenei* (Manter, 1934) Manter, 1935.
Host: *Monolene antillarum.*

116. *Lomasoma wardi* (Manter, 1934) Manter, 1935.
Hosts: *Coelorhynchus carminatus*, Grenadier; *Urophycis regius.*

117. *Megenteron crassum* Manter, 1934.
Host: *Diplacanthopoma brachysoma.*

118. *Steringophorus magnus* Manter, 1934.
Host: Unidentified eel.

119. *Steringophorus profundus* Manter, 1934.
Host: *Argentina striata.*

Family HAPLOSPLANCHNIDAE

120. *Haplosplanchnus acutus* (Linton, 1910) Manter, 1937.
Hosts: *Strongylura raphidoma*, Houndfish; *Strongylura timucu*, Houndfish.

121. *Haplosplanchnus adacutus* Manter, 1937.
Hosts: *Abudefduf marginatus*, Sergeant major; *Halichoeres bivittatus*, Slippery dick; *H. maculipinna*, Slippery dick.

122. *Haplosplanchnus brachyurus* Manter, 1937.
Hosts: *Cryptotomus auropunctatus*, Parrotfish; *Pseudoscarus guacamaia*, Rainbow parrotfish; *Pseudoscarus coelestinus*, Parrotfish; *Sparisoma aurofrenatum*, Parrotfish; *S. spinidens*, Parrotfish; *S. viride*, Parrotfish.

123. *Haplosplanchnus kyphosi* Manter, 1947.
Hosts: *Kyphosus sectatrix*, Bermuda chub; *H. incisor*, Yellow chub.

124. *Haplosplanchnus obtusus* (Linton, 1910) Manter, 1937.
Hosts: *Acanthurus coeruleus*, Blue tang; *A. hepatus*, Doctorfish.

125. *Haplosplanchnus pomacentri* Manter, 1937.
Hosts: *Pomacentrus leucostictus*, Beau gregory; *P. xanthurus*, Beau gregory.

126. *Haplosplanchnus sparisomae* Manter, 1937.
Hosts: *Sparisoma pachycephalum*, Parrotfish; *P. viride*, Parrotfish.

Family MONORCHIDAE

127. *Genolopa ampullacea* Linton, 1910.
Hosts: *Bathystoma striatum; B. rimator*, Tomtate; *Brachygenys chrysargyreus*, Bronze grunt; *Haemulon album*, Margate fish; *H. carbonarium*, Caesar grunt; *H. flavolineatum*, French grunt; *H. macrostomum*, Gray grunt; *H. plumieri*, White grunt; *H. sciurus*, Yellow grunt; *Synodus foetens*, Lizardfish.

128. *Hurleytrema chaetodoni* Manter, 1942.
Hosts: *Chaetodon capistratus*, Butterfly fish; *C. ocellatus*, Butterfly fish.

129. *Hurleytrema eucinostomi* Manter, 1942.
Host: *Eucinostomus lefroyi*, Mojarra.

130. *Monorchis latus* Manter, 1942.
Hosts: *Anisotremus virginicus*, Porkfish; *Haemulon plumieri*, White grunt.

131. *Paraproctotrema brevicaecum* Manter, 1942.
Host: *Caranx bartholomaei*, Yellow jack.

132. *Postmonorchis orthopristis* Hopkins, 1941.
Host: *Haemulon flavolineatum*, French grunt.

133. *Proctotrema longicaecum* Manter, 1940.
Host: *Anisotremus virginicus*, Porkfish.

134. *Proctotrema truncatum* (Linton, 1910) Manter, 1940.
Hosts: *Haemulon album*, Margate fish; *H. flavolineatum*, French grunt; *H. plumieri*, White grunt; *H. sciurus*, Yellow grunt.

135. *Proctotrema parvum* Manter, 1942.
Host: *Haemulon flavolineatum*, French grunt.

Family BIVESICULIDAE

136. *Bivesicula hepsetiae* Manter, 1947.
Host: *Hepsetia stipes*, Hardhead.

Family GORGODERIDAE

137. *Phyllodistomum carangis* Manter, 1947.
Host: *Caranx ruber*, Runner.

138. *Xystretrum solidum* Linton, 1910.
Hosts: *Balistes capriscus*, Triggerfish; *Lactophrys triqueter*, Trunkfish.

139. *Xystretrum pulchrum* (Travassos, 1921) Manter, 1947.
Host: *Sphoeroides splengleri*, Southern puffer.

Family MEGAPERIDAE

140. *Megapera gyrina* (Linton, 1907) Manter, 1934.
Host: *Lactophrys tricornis*, Trunkfish.

141. *Megapera orbicularis* (Manter, 1933) Manter 1934.
Host: *Lactophrys tricornis*, Trunkfish.

142. *Megapera ovalis* (Manter, 1933) Manter, 1934.
Host: *Monacanthus hispidus*, Filefish.

143. *Megapera pseudura* (Manter, 1933) Manter, 1934.
Host: *Lactophrys tricornis*, Trunkfish.

144. *Thysanopharynx elongatus* Manter, 1933.
Host: *Lactophrys tricornis*, Trunkfish.

Family CRYPTOGONIMIDAE

145. *Siphodera vinaledwardsii* (Linton, 1899) Linton, 1910.
Host: *Ocyurus chrysurus*, Yellowtail.

146. *Metadena crassulata* Linton, 1910.
Host: *Lutjanus analis*, Muttonfish.

147. *Metadena globosa* (Linton, 1910) Manter, 1947.
Host: *Lutjanus griseus*, Gray snapper.

148. *Metadena adglobosa* Manter, 1947.
Host: *Lutjanus griseus*, Gray snapper.

149. *Metadena brotulae* (Manter, 1934) Manter, 1947.
Hosts: *Brotula barbata; Lophius piscatorius*, Angler fish.

Family HEMIURIDAE

150. *Hemiurus* sp. of Manter, 1934.
Host: *Peristedion imberbe.*

151. *Parahemiurus merus* (Linton, 1910) Woolcock, 1935.
Hosts: *Abudefduf saxatilis*, Sergeant major; *Harengula clupeola*, Pilchard; *Ocyurus chrysurus*, Yellowtail; *Synodus foetens*, Lizardfish; *Trachurops crumenophthalmus*, Goggle-eye jack.

152. *Anahemiurus microcercus* Manter, 1947.
Hosts: *Calamus bajonado*, Jolt-head porgy; *C. calamus*, Saucer-eye porgy; *Eucinostomus lefroyi*, Mojarra.

153. *Lecithochirium mecosaccum* Manter, 1947.
Hosts: *Synodus foetens*, Lizardfish; *S. poeyi*, Lizardfish.

154. *Lecithochirium microstomum* Chandler, 1935.
Hosts: *Ancylopsetta dilecta*, Flounder; *Promicrops itaiara*, Jewfish; *Megalops atlanticus* Tarpon.
Reported also by Chandler (1935) from *Trichiurus lepturus*, Cutlass fish, in Galveston Bay and from the same host at Grand Isle, La., by Melugin (1940).

155. *Lecithochirium* sp. of Manter, 1934.
Host: *Urophycis regius.*

156. *Lecithochirium texanum* (Chandler, 1941) Manter, 1947.
Host: *Sarda sarda*, Bonito.
Reported by Chandler (1941) from Texas coast near Freeport.

157. *Sterrhurus floridensis* Manter, 1934.
Hosts: At least 21 species of fishes at Tortugas (see Manter, 1947).

158. *Sterrhurus fusiformis* (Luhe, 1901) Looss, 1907.
Hosts: *Gymnothorax moringa*, Spotted moray; *G. funebris*, Black moray.

159. *Sterrhurus microcercus* Manter, 1947.
Host: *Fistularia tubaccaria*, Trumpet fish.

160. *Sterrhurus praeclarus* Manter, 1934.
Host: *Merluccius* sp.

161. *Dissosaccus laevis* (Linton, 1898) Manter, 1947.
Hosts: *Helicolenus maderensis*; *Peristedion longispathum*; *P. miniatum*; *P. platycephalum.*

162. *Lethadena profunda* (Manter, 1934), Manter 1947.
Hosts: *Pronotogrammus aureorubens*; *Xenodermichthys capei.*

163. *Adinsoma robustum* (Manter, 1934) Manter, 1947.
Hosts: *Chaunax pictus*, Frogfish; *Chlorophthalmus truculentus*; *Merluccius* sp.; *Paralichthys oblongus*, Flounder; *Urophycis chesteri*; *U. regius.*

164. *Ectenurus virgulus* Linton, 1910.
Hosts: *Bothus ocellatus*, Flounder; *Harengula clupeola*, Pilchard; *Trachurops crumenophthalmus*, Goggle-eye jack.

165. *Parectenurus americanus* Manter, 1947.
Hosts: *Caranx bartholomaei*, Yellow jack; *Synodus foetens*, Lizardfish.

166. *Dinurus tornatus* (Rud., 1819) Looss, 1907.
Host: *Coryphaena hippurus*, Dolphin.

167. *Dinurus breviductus* Looss, 1907.
Host: *Coryphaena hippurus*, Dolphin.

168. *Dinurus longisinus* Looss, 1907.
Host: *Coryphaena hippurus*, Dolphin.

169. *Dinurus barbatus* (Cohn, 1903) Looss, 1907.
Host: *Coryphaena hippurus*, Dolphin.

170. *Dinurus scombri* Yamaguti, 1934.
Host: *Euthynnus alletteratus*, Little tuna.

171. *Stomachicola rubea* (Linton, 1910) Manter, 1947.
Hosts: *Gymnothorax funebris*, Black moray; *G. moringa*, Moray.
Reported from *Synodus foetens* at Grand Isle, La., by Melugin (1940). It also occurs at Tortugas (Linton, 1910).

172. *Aponurus laguncula* Looss, 1907.
Host: *Ocyurus chrysurus*, Yellowtail.

173. *Aponurus intermedius* Manter, 1934.
Hosts: *Chaunax pictus;* unidentified eel; unidentified sole.

174. *Brachadena pyriformis* Linton, 1910.
Hosts: *Bathystoma striatum; Brachygenys chrysargyreus*, Bronze grunt; *Calamus bajonado*, Jolt-head porgy; *Chaetodon aya*, Butterfly fish; *C. sedentarius*; *Haemulon album*, Margate fish; *H. macrostomum*, Gray grunt; *H. parra*, Sailor's choice; *H. plumieri*, White grunt; *Ogcocephalus cubifrons*, Batfish.

175. *Lecithaster acutus* (Linton, 1910) Manter, 1947.
Hosts: *Acanthurus hepatus*, Doctor fish; *A. caeruleus*, Blue tang.

176. *Leurodera decora* Linton, 1910.
Hosts: *Anisotremus virginicus*, Porkfish; *Brachygenys chrysargyreus*, Bronze grunt; *Haemulon carbonarium*, Caesar grunt; *H. parra*, Sailor's choice; *H. plumieri*, White grunt; *H. sciurus*, Yellow grunt; *H. flavolineatum*, French grunt; *Lutjanus griseus*, Gray snapper; *Acanthurus hepatus* (?), Doctor fish.

177. *Theletrum fustiforme* Linton, 1910.
Host: *Pomacanthus arcuatus*, Black angelfish.
Reported also from *P. arcuatus* and *P. paru*, French angelfish, from the north coast of Cuba by Vigueras (1940a).

178. *Derogencs crassus* Manter, 1949.
Host: *Callionymus agassizii*.

179. *Derogenes varicus* (Mueller, 1784) Looss, 1901.
Hosts: *Helicolenus maderensis; Merluccius* sp.; *Scorpaena cristulata; Setarches parmatus; Urophycis regius*.

180. *Gonocerca crassa* Manter, 1934.
Hosts: *Ancylopsetta dilecta; Brotula barbata; Coelorhynchus carminatus; Lophius piscatorius; Merluccius* sp.,; *M. bilinearis; Paralichthys oblongus; Paralichthys* sp.; *P. squamilentus; Phycis cirratus; Saurida normani; Setarches parmatus; Synodontid; Synodus intermedius; Urophycis regius*.

181. *Gonocerca phycidis* Manter, 1925.
Hosts: *Coelorhynchus carminatus*, Grenadier; *Merluccius* sp.; *Urophycis regius*.

182. *Gonocercella atlantica* Manter, 1940.
Host: *Monacanthus hispidus*, Filefish.

183. *Parasterrhurus anurus* Manter, 1934.
Host: *Argentina striata*.

184. *Hemiperina nicolli* Manter, 1934.
Hosts: *Chaunax pictus*, Frogfish; *Dibranchus atlanticus; Diplacanthopoma brachysoma*.

185. *Hysterolecitha rosea* Linton, 1910.
Hosts: *Acanthurus bahianus*, Ocean tang; *A. caeruleus*, Blue tang; *A. hepatus*, Doctor fish.

186. *Macradena perfecta* Linton, 1910.
Host: *Acanthurus caeruleus*, Blue tang.

187. *Macradenina acanthuri* Manter, 1947.
Host: *Acanthurus caeruleus*, Blue tang.

188. *Opisthodena dimidia* Linton, 1910.
Hosts: *Kyphosus sectatrix*, Bermuda chub; *K. incisor*, Yellow chub.

189. *Dictysarca virens* Linton, 1910.
Host: *Gymnothorax funebris*, Black moray

190. *Hirudinella ventricosa* (Pallas, 1774) Baird, 1853.
Host: *Coryphaena hippurus*, Dolphin.

191. *Sclerodistomum sphoeroidis* Manter, 1947.
Host: *Sphoeroides spengleri*, Southern puffer

192. *Tetrochetus coryphaenae* Yamaguti, 1934.
Host: *Coryphaena hippurus*, Dolphin.

193. *Prosogonotrema bilabiatum* Vigueras, 1940.
Host: *Ocyurus chrysurus*, Yellowtail.
Reported from north coast of Cuba by Vigueras (1940b).
Vigueras considered it in a new family.

Family APOROCOTYLIDAE

194. *Deontacylix ovalis* Linton, 1910.
Hosts: *Kyphosus sectatrix*, Bermuda chub; *K. incisor*, Yellow chub.

195. *Cardicola cardiocolum* (Manter, 1947) Short, 1953.

196. *Cardicola laruei* Short, 1953.
Host: *Cynoscion arenarius*, White trout; *C. nebulosus*, Speckled trout.

HOST SPECIFICITY OF TREMATODES OF MARINE FISHES OF THE GULF OF MEXICO

Monogenea are rather highly specific in regard to their hosts. Most species are known to infect in nature only a single host species. If there are several hosts they are usually related.

Host specificity among the Digenea varies considerably. It is not marked among a number of species infecting birds and mammals. Judging from the collection records at Tortugas, trematodes of fishes there have very considerable host specificity. Considered from the species level of 189 species collected (Manter 1947) 105 or 55.5 percent were found in only 1 species of host; 43 from 2 hosts, 14 from 3 hosts, etc., although 1 species occurred in 14 hosts, 1 in 16 hosts, and 1 in 21 hosts. While it must be admitted that nonoccurrence of a trematode within a certain species of host does not necessarily mean it cannot infect that host, data derived from numerous examinations indicate rather clearly that such species do not do so under natural conditions. The fishes studied were mostly shallow-water species living not far from one another. The fact that a few species do in fact infect a wide variety of hosts indicates that food habits are not necessarily a barrier. The only experimental testing of host specificity in this region was that by McCoy (1930) who found that *Hamacreadium mutabile* and *H. gulella* developed only in three species of the snapper family, Lutjanidae, and did not infect

any of five other species of fishes belonging in five other families.

If a trematode species occurs in 2 or several hosts, the hosts are usually related. For example, 138 trematode species (73 percent of those collected) were limited to a single host genus. Only rarely is a trematode species found in fishes belonging in different families. Little is known regarding the host specificity of larval stages for their intermediate hosts. It is sometimes greater, particularly for the molluscan host, than that of the adult parasite.

This tendency of trematodes to occur in a limited number of hosts which are usually related gives added interest to the geographical distribution of these parasites. During my study of Tortugas trematodes, I was frequently impressed to discover that the hosts of the same or a related trematode in distant oceans proved to be a fish related to the host at Tortugas.

GEOGRAPHICAL DISTRIBUTION OF TREMATODES OF FISHES AT TORTUGAS, FLORIDA

TREMATODES FROM 50 FATHOMS OR BELOW

Systematic dredgings south of Loggerhead Key under the direction of Dr. W. H. Longley in the summers of 1930–32 presented an unusual opportunity for collection of trematode parasites down to depths of some 500 fathoms (Manter, 1934). It was found that fishes down to that depth were as commonly infected as fishes of shallow (surface) waters, 49 species being collected from about 90 species of fishes. These trematodes are almost entirely different species from those occurring in the nearby surface water; only 3 species from below 100 fathoms occurred in lesser depths and 2 of these are atypical (*Distomum fenestratum* is an immature, very nonspecific species, while *Sterrhurus floridensis* has so little host specificity that precocious maturity in a crustacean host is suggested). Even at 50 fathoms only 3 additional species (*Deretrema fusillus*, *Myzoxenus vitellosus*, and *Helicometrina nimia*) occur in surface waters at Tortugas. This marked difference in the deeper water fauna might be expected since the fishes and invertebrates are also different species.

A more interesting aspect of the deeper water trematode fauna is the affinity it shows for distant, cool or cold water faunas. Manter (1934) noted a number of species found only at 50 fathoms or below at Tortugas but known from surface waters of the North Atlantic. Studies since 1934 add 2 species which do extend into surface waters at Tortugas and some 6 species found in distant oceans. The following table shows the distribution of these species. Numbers in parentheses indicate the number of host species involved. The table is based on a total of 41 adult species definitely identified.

TABLE 1.—*Distribution of trematode fauna*

Species	Depth	Other localities
	fathoms	
a. Species reported elsewhere (1934)		
Helicometra fasciata (3)	50–60	Great Britain (10). European (20). Mexican Pacific (2).
Derogenes varicus (5)	125–200	Maine coast (6). North Atlantic (many). North Pacific (many). Galapagos Islands (1).
Dissosaccus laevis (4)	165–200	Woods Hole (1), deepwater.
Gonocerca phycidis (3)	160–300	Maine coast (1).
Lepidapedon elongatum (4)	160–300	Maine coast (6). British Isles (1). Woods Hole (6). Now known from Japan (1).
Lepidapedon rachion (1)	200–325	Maine coast (1). British Isles (4). Woods Hole (4).
Sterrhurus floridensis (8)	50–197	Tortugas (shallow), (many).
b. Species reported elsewhere since 1934		
Deretrema fusillum (1)	50	Woods Hole (1). Tortugas, shallow (1).
Derogenes crassus (1)	90	Japan (1), deepwater (?). Tasmania (1), shallow.
Gonocerca crassa (12)	40–300	Japan (1), deepwater (?).
Lecithochirium microstomum (1)	100	Tortugas (1), shallow.
Lepidapedon nicolli (1)	90	Mexican Pacific (1), shallow.
Myzotus vitellosus (1)	50–60	Tortugas (1), shallow.
Prosorhynchus ozakii (1)	90	Mexican Pacific (1), shallow.
Pseudopecoeloides vulgaris (16)	50–315	Puget Sound (1), shallow.

The above data suggest that a bathymetric barrier between the trematode faunas of surface waters and of depths 100 fathoms or more at Tortugas is more effective than any existing between the deeper fauna and distant cool oceans. The deep-sea fauna itself is evidently very widespread, but a number of its trematode species occur in more shallow depths near or in the Arctic and Antarctic Seas.

The above comparisons have been on the species level. It is of some further interest to note that of 13 new genera named in 1934 from deep water at Tortugas, 7 involving 15 species have since been reported elsewhere as follows: One (1 species) from Woods Hole; four (11 species) from Japan; two (3 species) from Tasmania. The species from Tasmania were in shallow-water fishes.

A remarkable incident occurred in connection with *Lepidapedon nicolli* and *Prosorhynchus ozakii*. These two species, new at the time, both occurred at Tortugas at 90 fathoms in the same individual fish, a snowy grouper, *Epinephelus niveatus*. In 1934, I collected these same two species again from a single fish, an "unidentified, spotted, grouper-like fish" from the Pacific Ocean at Isabel Island, Mexico. It is unfortunate that this fish could not be further identified. As far as I can learn, *Epinephelus niveatus* does not occur in the Pacific.

TREMATODES FROM SURFACE WATER FISHES

A comparison of 142 species of trematodes from less than 50 fathoms at Tortugas with faunas known elsewhere reveals, in general, (1) that the Tortugas fauna is very unlike that of the coast of Maine or Massachusetts, the European Atlantic or the Mediterranean, and (2) it is strikingly similar to the fauna at Bermuda and the tropical Amercian Pacific.

Of the 142 species at Tortugas, 28 species (19.8 percent) occur at Bermuda (Hanson 1950). This similarity is to be expected since many of the same species of fishes occur in both regions. In fact, at least 21 of the 28 species of trematodes occur in the same host species in both regions.

The only other part of the world where such trematodes have been collected sufficiently to give adequate sampling and which compares with the similarity to Bermuda is the tropical American Pacific. Considering species from 50 fathoms or less, 24 or 16.8 percent of 142 Tortugas species occur in the American Pacific. Also, there is reason to believe this similarity is even greater than this figure indicates. Three additional species in the Pacific occur in Bermuda fishes which occur at Tortguas; still three more species are now reported (Pearse 1949) from Beaufort, N. C., in fishes which occur at Tortugas. Thus, the probable total is at least 30 species, a figure practically identical with that derived from comparison with Bermuda. Furthermore, if fishes down to 100 fathoms were considered, the Pacific percentage would be slightly higher.

Thus, based on our present knowledge, one can conclude that the Tortugas trematode fauna of surface-water fishes is very similar to that of Bermuda, as would be expected, and equally as similar to that of the tropical American Pacific, as might not be expected. There is one striking difference among these regions. Whereas at Bermuda the species of host fishes are, in general, identical with those involved at Tortugas, in the Pacific the hosts are, with very few exceptions, different but related species. As far as the trematodes are concerned, the tropical American Pacific occupies a position comparable to that of Bermuda in relation to Tortugas, almost as though there were no land barrier between the two oceans. It is well known that this land barrier has not always existed. Have the trematode parasites retained their specific identity while their hosts, perhaps both fish and molluscan, have evolved into slightly different species? Trematode distribution suggests that just as the Gulf Stream has made Bermuda practically an outpost of the Gulf of Mexico and Caribbean faunas, the tropical and subtropical American Pacific is also such an outpost persisting as evidence of the prehistoric continuity of the two oceans.

Further evidence of an ancient influence of inter-oceanic continuity is the relative dissimilarity of the Tortugas fauna to such adjacent regions as Beaufort, N. C. Here the trematodes have been as well sampled as in the Pacific, and only 15 of the Tortugas species are known there. This number is hardly more than half the number known to occur in the Pacific. If the trematodes were accidentally distributed by migrants such as birds, this difference would not be expected. Fourteen Tortugas species, from less than 50 fathoms, occur at Woods Hole, Mass. Eleven occur in Japanese waters. This extension of species far into the Pacific is reflected in the Bermuda fauna. Five of the Bermuda species occur in Japan and six in the tropical American Pacific, as compared with seven at much nearer Woods Hole, six at Beaufort, three in the European Atlantic, and three in the Mediterranean (Hanson 1950). This greater affinity of the Bermuda trematodes for Japanese than for European waters is better understood in the light of the Pacific affiinities of the Tortugas fauna.

The distribution of these trematodes is, of course, a result of numerous and complex factors. For example, a few of the species considered here are parasites of open sea fishes with a very wide range. Their parasites would be expected to have a wide distribution. Omission of these species, however, would not materially change the

proportional figures. The species from deeper water were considered separately because parasites from these depths have not been studied in most regions. Presumably, these species have a wide distribution at appropriate depths. If sufficient numbers of species are involved, the exceptional cases or errors in identification will be minimized. In most cases, such factors would probably more or less balance one another in the various localities. However, it seems to me that the figures available are not suitable for statistical analysis because of factors which cannot be given numerical value. For example, from purely geographical considerations one would expect the Pacific fauna to be very different from Tortugas, separated as it is by a land barrier and with practically no possibility of contact by way of the Antarctic or the partly fresh-water Panama Canal. More complete knowledge of these parasites in all regions is needed. As this knowledge is gained it seems probable that a very interesting host-parasite-distribution picture will unfold, particularly at the specific and generic levels.

TREMATODES OF TURTLES

Four species of marine turtles occur in the Gulf of Mexico. These are the loggerhead turtle, *Caretta caretta*, the green turtle, *Chelonia mydas*, the hawk-bill turtle, *Eretmochelys imbricata*, and the leathery or leatherback turtle, *Dermochelys coriacea*. All four of these turtles have a very wide distribution in warm seas. They are very favorable hosts for trematodes, some of which also appear to be widely distributed, others being reported as yet only from certain localities. The actual distribution of these trematodes can be known only after the examinations made in various regions are more or less equivalent. Until then, the presence of a species is more significant than its apparent absence. With only two exceptions, the trematodes described from marine turtles are all Digenea. Since a molluscan host is also required in their life cycle it is probable that a number of these trematodes will have a distribution limited by the distribution of the molluscan host.

Considering the wide individual range of these turtles in the open sea, a surprising variety of trematodes succeed in parasitizing them. Fifty-one species have been reported from *Chelone mydas*, 30 from *Caretta caretta*, and 9 from *Eretmochelys imbricata*. It is an interesting fact that none of these trematodes is known to occur as an adult parasite of fishes.[1] Furthermore, despite the aquatic life of the turtles, these trematodes belong to reptilian parasitic groups (families and genera). Turtles have no representatives of such common trematode families of fishes as Hemiuridae, Opecoelidae, Fellodistomatidae, etc. A similar situation exists in connection with the trematodes of marine mammals which are quite different from species occurring in either turtles or fishes.

Only a few turtles from the Gulf have been examined for parasites. Additional records, particularly from *Chelone* and *Eretmochelys*, could easily be made. Such records would make possible comparisons between the parasites of this region and other seas.

TREMATODES OF CARETTA CARETTA

Fifteen species of trematodes from *Caretta caretta* at Tortugas, Fla., have been reported by Linton (1910), Pratt (1914), Manter (1932), and Luhman (1935). These are as follows:

ASPIDOGASTREA

Aspidogastridae

1. *Lophotaspis vallei* (Stossich, 1899) Looss, 1902.

DIGENEA

Pronocephalidae

2. *Cricocephalus albus* (Kuhl & van Hasselt, 1822) Looss, 1899.
3. *Diaschistorchis pandus* (Braun, 1901) Johnston, 1913.
4. *Pleurogonius trigonocephalus* (Rud., 1809) Looss, 1901.
5. *Pyelosomum longicaecum* Luhman, 1935.

Brachycoeliidae

6. *Cymatocarpus undulatus* Looss, 1899.
7. *Orchidasma amphiorchis* (Braun, 1899) Braun, 1901.

Plagiorchidae

8. *Pachypsolus ovalis* Linton, 1910.
9. *Pachypsolus tertius* Pratt, 1914.
10. *Styphlotrema solitarius* (Looss, 1899) Odhner, 1910.

Rhytidodidae

11. *Rhytidodes secundus* Pratt, 1914.

Gorgoderidae

12. *Phyllodistomum cymbiforme*, (Rud., 1819) Braun, 1899.

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[1] The presence of a single specimen of *Orchidasma amphiorchis* in *Coryphaena hippurus* reported by Manter (1931) is without doubt an accidental and temporary condition probably due to recent ingestion of a young turtle by the fish.

DIGENEA—Continued

SPIRORCHIDAE

13. *Hapalotrema synorchis* Luhman, 1935.
14. *Neospirorchis pricei* Manter & Larson, 1950.
15. *Carettacola bipora* Manter & Larson, 1950.

Five of these species (*Pyelosomum longicaecum*, *Pachypsolus ovalis*, *P. tertius*, *Rhytidoeds secundus*, and *Hapalotrema synorchis*) are known as yet only from the Gulf of Mexico.

TREMATODES OF CHELONIA MYDAS, THE GREEN TURTLE

Lists by Hughes, Higginbotham, and Clary (1941) and Ruiz (1946) show that 51 species of trematodes have been reported from *Chelonia mydas* in various parts of the world. Of these, 10 species or about one-fifth of the total, are also known from *Caretta caretta*. I believe no other species of host is known to harbor as many as 50 species of trematodes. Surely, no other reptile approaches this number.

No definite records of species have been published from this host in the Gulf of Mexico. Manter (1930) states that he collected three species of trematodes from *Chelonia* at Tortugas but had not then identified them. This collection is still incompletely studied. Two of the species, however, can be reported as *Desmogonius desmogonius* Stephens, 1911, known from the same host from the coast of Nicaragua; and *Polyangium linguatula* (Looss 1899) Looss 1900, known from the Mediterranean and from Brazil. More examinations of *Chelonia mydas* will, without doubt, reveal additional species in Gulf waters. Ruiz (1946) reports 10 species from this host from the coast of Brazil. Price (1939a) reports *Rhytidodoides intestinalis* Price, 1939, and *R. similis* Price, 1939, from a *Chelonia mydas* which died in the Washington Zoo but does not state the origin of the turtle.

TREMATODES OF ERETMOCHELYS IMBRICATA, THE HAWK-BILL TURTLE

Apparently only one trematode has been reported from this turtle in the Gulf region. It is *Diaschistorchis pandus* (Braun) reported from Cuba by Vigueras (1935). This trematode has an almost world-wide distribution and also infects *Caretta caretta* and *Chelonia mydas*. Five species of trematodes are known from *E. imbricata* from Japanese waters, two from Australia, one from Bermuda, and one from Ireland.

TREMATODES OF DERMOCHELYS CORIACEA, THE LEATHERY OR LEATHERBACK TURTLE

Apparently only one species of trematode, *Pyelosomum renicapite* (Leidy 1856) Ruiz 1946, has been recorded from this turtle and none from the Gulf of Mexico. However, Dr. A. C. Chandler informs me (by correspondence) he has collected this species of trematode from a leather-back turtle washed up near Galveston, Texas, some years ago.

TREMATODES OF BIRDS OF THE GULF OF MEXICO

Almost no study of trematodes collected from birds from the Gulf of Mexico has been made. Obviously such trematodes must be numerous. It seems beyond the scope of this paper to assemble the scattered records of trematodes collected elsewhere even from birds which occur in the Gulf.

Pratt (1911), Linton (1928), and Manter (1930) all mention *Galactosomum cochleariforme* (Rud.) as present in *Fregata magnificens*, the man-of-war bird, at Tortugas, and Chandler (1951) recorded *Galactosomum fregatae* and a new strigeid, *Schwartzitrema seamsteri*, from a specimen of this bird near Corpus Christi, Tex.

Records from oceanic birds from the Caribbean region include:

Galactosomum johnsoni Price, 1934, from *Sula leucogastra*, brown booby, from Puerto Rico.

Galactosomum fregatae Prudhoe, 1949, from *Fregata magnificens*, man-of-war bird, from Trinidad.

Galactosomum darbyi Price, 1934, from *Pelecanus occidentalis*, brown pelican, from Dominican Republic.

Mesostephanus appendiculatoides (Price, 1934) Lutz, 1935, from *Pelecanus occidentalis*, brown pelican, from Dominican Republic.

Mesostephanus fajardensis (Price, 1934) Lutz, 1935, from *Sula leucogaster*, brown booby, from Puerto Rico.

TREMATODES OF MAMMALS

Marine mammals, particularly dolphins and whales, are commonly infected with trematodes. No collections from such hosts, however, appear to have been made in the Gulf of Mexico.

Sokoloff and Caballero (1932) described a trematode, *Schizamphistoma manati* from a manatee,

Manatus latirostris, from the delta of the Panuco River, near Tampico, Mexico.

STUDIES ON LARVAL STAGES AND LIFE CYCLES OF TREMATODES OF THE GULF OF MEXICO

Miller (1925, 1926, 1927, 1929) and Miller and McCoy (1929) have studied cercariae collected chiefly from snails from coral reefs near the Biological Laboratory at Tortugas. Most of these studies were on the behavior of the cercariae and only brief preliminary descriptions of the cercariae were given. The cercariae were named alphabetically as Cercaria A, Cercaria B, etc. In 1929, Cercaria P was referred to as *Cercaria floridensis*. As is usual among marine mollusks, only a small percentage of individuals are infected. During the first season (1925) Miller examined 4,341 mollusks belonging to 33 genera and including 50 species and varieties, and found only 45 individuals including 9 species infected. Miller's later work indicates that the incidence of infection may vary greatly from year to year. Altogether, 22 species of cercariae were studied. The type of each cercaria is indicated. The following list includes the mollusks found infected and the cercariae found in each:

Astrea americana
- Cercaria A---------- cotylocercous.
- Cercaria B---------- cotylocercous.

Astrea longispina
- Cercaria C---------- immature sporocysts.

Cerithium litteratum
- Cercaria D---------- gymnocephalous.
- Cercaria E---------- gymnocephalous.
- Cercaria F---------- huge-tailed monostome.
- Cercaria G---------- Xiphidiocercaria.
- Cercaria P---------- binoculate, lophocercous.
- Cercaria Q---------- trioculate monostome.
- Cercaria R---------- large furcocercous.
- Cercaria S---------- distome, gymnocephalous.
- Cercaria T---------- huge-tailed monostome.
- Cercaria U---------- huge-tailed monostome.
- Cercaria W---------- huge-tailed monostome.

Cerithium algicola
- Cercaria H---------- gymnocephalous.

Columbella mercatoria
- Cercaria I---------- cotylocercous (?)
- Cercaria J---------- cotylocercous.

Crepidula aculeata
- Cercaria K---------- trichocercous.
- Cercaria L---------- cystophorous.

Glyphis listeri
- Cercaria M---------- cotylocercous.

Pinna carnea
- Cercaria N---------- gasterostome.

Thais deltoidea
- Cercaria O---------- echinostome.

Except for the life cycles studied by McCoy (1929, 1930) little attempt has been made to associate these cercariae with adult trematodes. The problem is usually difficult because many characters used in classification do not appear in the cercaria. The mollusks studied might be infected with trematodes from such birds as the pelican, tern, or frigate bird, or from marine turtles, as well as from fishes. McCoy proved that Cercaria A developed into *Hamacreadium mutabile*, and Cercaria B into *Hamacreadium gulella*. He believed Cercaria P developed into some species of *Acanthochasmus*. Second intermediate hosts were *Thalassoma bifasciatus*, bluehead, or *Halichoeres bivittatus*, slippery dick. Manter (1932, 1933a) found that Cercaria J from *Columbella mercatoria* penetrated into and encysted in the shrimp, *Lysmata intermedia*. He found in this same shrimp and in *Crangon formosum* the metacercariae of *Helicometrina nimia*. He also pointed out that Cercaria L greatly resembles a common juvenile trematode known as *Distomum fenestratum*.

Schechter (1943) reports cercariae of *Parorchis acanthus* from the oyster-drilling snail, *Thais floridana haysae* from Barataria Bay, La. The adult of this echinostomid trematode is a parasite of birds, *e. g.*, the herring gull, *Larus argentatus*. It has been reported from Cuba by Vigueras (1940a) from the flamingo, *Phoenicopterus ruber*, and from *Nycticorax nycticorax hoactli*.

Cable and McLean (1943) described a "rattenkonig" cercaria, *C. clausii* Monticelli, from the gastropod, *Lamellaria leucosphaera*, from the west coast of Florida. Miller (1929) described the same colonial aggregation of individuals for his Cercaria W from *Cerithium litteratum* at Tortugas.

Larval stages of gasterostomes are common parasites of bivalves. Oysters both of the Atlantic and Gulf coasts are commonly infected with such larvae. Pearse and Wharton (1938) reported "*Bucephalus gracilescens* (Rudolphi)" from oysters in Apalachicola Bay, Fla. A study of these gasterostome larvae in oysters of the Gulf of Mexico is being made by Sewell H. Hopkins of Texas A. and M. Research Foundation.

The miracidium of *Lophotaspis vallei*, an aspidogastrid of the loggerhead turtle was studied by Manter (1932). Wharton (1939) discovered that a juvenile stage of this trematode occurred in the flag conch, *Fasciolaria gigas*, collected in Gulf County, Fla. As Wharton indicated, miracidia doubtless penetrate the conch and develop without reproduction to the infective stage. Turtles would thus become infected by eating infected conchs.

SUMMARY

Over 200 species of Trematoda reported from fishes of the Gulf of Mexico include 10 species of Monogenea, 2 species of Aspidogastrea, and 196 species of Digenea. Of the Digenea, 18 species are gasterostomes, 178 species are prosostomes. Most of these trematodes have been studied only from the eastern portion of the Gulf at Tortugas, Fla.

Trematodes of other vertebrates of the Gulf have been studied very little. Fifteen species have been reported from *Caretta caretta*, the loggerhead turtle, at Tortugas. Two species are reported in this paper from *Chelonia mydas*, the green turtle. Three species of Trematoda are known in the Gulf. At least five other species have been reported from oceanic birds in the Caribbean, birds which are also common in the Gulf.

Larval stages of trematodes in mollusks of the Gulf include 22 species of cercariae at Tortugas. Cercariae of *Parorchis acanthus* have been reported from *Thais floridana* from the Louisiana coast. Here also oysters are commonly infected with gasterostome larvae.

Only three life cycles are known. *Hamacreadium mutabile* and *H. gulella*, adults of which occur in Lutjanidae (snappers), develop in a snail, *Astrea americana*, and then utilize *Thalassoma bifasciatus*, bluehead, or *Halichoeres bivittatus*, slippery dick, as second intermediate host. Juvenile stages of *Lophotaspis vallei* from the loggerhead turtle infect the flag conch, *Fasciolaria gigas*.

A discussion of geographical distribution of trematodes of fishes points out (1) that the trematodes of fishes from 100 fathoms or deeper show practically no affinity to trematodes of surface waters of the Gulf but do show considerable affinity to species from fishes of distant but cold waters, (2) the trematode fauna of surface waters (less than 50 fathoms) shows a marked similarity to such faunas at Bermuda and in the tropical American Pacific, a similarity approximately twice as great as is shown to Beaufort, N. C., or Woods Hole, Mass. Further study of this phenomenon, at both the generic and specific level, is suggested.

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CESTODA

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The first work on cestodes of Gulf fishes was done by Linton on material collected by him at the Biological Laboratory of the Carnegie Institution at Dry Tortugas, Florida, in the summers of 1906–1908. They are discussed in Linton (1908b, 1909). No further work was done until Chandler (1935a, 1935b) reported some observations on helminths of fish in Galveston Bay, Texas. Perez Vigueras (1936), in a report of helminths in Cuba, reported three unidentified larvae of Trypanorhyncha from teleosts off the province of Havana. Potter (1937) described one additional new species of cestode from Dry Tortugas, and Shuler (1938) reported on some cestodes collected from this same locality by Manter in 1930–1932, adding one more valid new species. Chandler (1942) reported on some cestodes from sharks taken near Englewood, Florida, adding two new species. Seamster (1950, personal communication) reported a few cestode infections from fishes taken in or near Corpus Christi Bay, Texas. Other than these few and incomplete investigations the cestodes of fishes in the Gulf of Mexico have not been studied. Further studies will undoubtedly yield many new species and bring to light interesting geographical relations with the fauna of the Caribbean Sea, the North Atlantic, and the Pacific Coast of Mexico. No cestodes have yet been reported from marine reptiles or mammals in the Gulf.

The cestode fauna so far known consists almost entirely of Tetraphyllidea and Trypanorhyncha which, as adults, parasitize practically all elasmobranchs in the Gulf and, as larvae, are found very commonly in the flesh or viscera of teleosts, often in such food fishes as members of the families Sciaenidae, Serranidae, and Lutjanidae. Although incapable of development in man they cause considerable economic loss because of popular antipathy to "wormy" fish. On the Texas coast the drum, *Pogonias cromis*, and to a lesser extent other sciaenid fishes, very frequently harbor the plerocerci of *Poecilancistrium robustum* or related species which are known to fishermen as "spaghetti worms" because of their great length. The adults of these worms are probably parasitic in a shark or ray as are other Trypanorhyncha. Some city health departments have considered banning drum from the markets because of their very frequent infestation, but the writer has counseled against this since these fish are an important cheap source of protein food.

TETRAPHYLLIDEA

Family DISCULICIPITIDAE

Disculiceps pileatus (Linton, 1890) Joyeux and Baer, 1935.
Host: *Carcharinus leucas*, cub shark.

Family CEPHALOBOTHRIIDAE

Hexacanalis (?) *marsupium* (Linton, 1916) Dollfus, 1948.
Host: *Stoasodon narinari*, spotted sting ray; Dry Tortugas (Linton).

Family PHYLLOBOTHRIIDAE

Phyllobrothrium foliatum Linton, 1890.
Host: *Dasyatus sabina*, southern sting ray; Dry Tortugas (Linton).

Phyllobothrium mustelis (van Beneden, 1850) (=*Orygmatobothrium angustum* Linton, 1890.)
Host: *Carcharinus leucas*, cub shark; Dry Tortugas (Linton).

Phyllobothrium lactuca van Beneden, 1850.
Host: *Negaprion brevirostris*, yellow shark; Dry Tortugas (Shuler).

Phyllobothrium dasybati Yamaguti, 1934.
Host: *Negaprion brevirostris*, yellow shark; Dry Tortugas (Shuler).

Phyllobothrium tumidum Linton, 1922.
Host: *Scoliodon terrae-novae*, sharp-nosed shark; Dry Tortugas (Shuler).

Phyllobothrium centrurum Southwell, 1925 (=*Anthocephalum gracile* Linton, 1890).
Host: *Dasyatis sabina*, southern sting ray; Dry Tortugas (Linton).

Phyllobothrium sp.
Host: *Dasyatis sabina*, southern sting ray; Corpus Christi Bay (Seamster).

Rhinebothrium flexile Linton, 1890.
Host: *Dasyatis sabina*, southern sting ray; Dry Tortugas (Linton).
Echeneibothrium minimum van Beneden, 1850.
Host: *Dasyatis sabina*, southern sting ray; Corpus Christi Bay (Seamster).
Anthobothrium laciniatum Linton, 1890.
Hosts: *Hypoprion brevirostris;* Dry Tortugas (Shuler); *Carcharinus leucas*, cub shark; Dry Tortugas (Linton).
Anthobothrium variabile (Linton, 1890) Southwell, 1925.
Host: *Dasyatis sabina*, southern sting ray; Dry Tortugas (Linton).
Anthobothrium sp.
Host: *Dasyatus sabina*, southern sting ray; Corpus Christi Bay (Seamster).

Family ONCHOBOTHRIIDAE

Acanthobothrium brevissime Linton, 1909.
Host: *Dasyatis sabina*, southern sting ray; Dry Tortugas (Linton).
Acanthobothrium coronatum (Rud., 1819) van Beneden, 1850 (=*Onchobothrium tortum* Linton, 1916).
Host: *Stoasodon narinari*, spotted sting ray; Dry Tortugas (Linton).
Acanthobothrium sp.
Host: *Dasyatis sabina*, southern sting ray; Corpus Christi Bay (Seamster).
Thysanocephalum thysanocephalum (Linton, 1889) Braun, 1900.
Host: *Galeocerdo cuvier*, tiger shark; Dry Tortugas (Linton).
Thysanocephalum rugosum Chandler, 1942.
Host: *Galeocerdo cuvier*, tiger shark; Englewood, Fla. (Chandler).
Cylindrophorus lasius (Linton, 1890) Southwell, 1925.
Host: *Carcharinus leucas*, cub shark; Dry Tortugas (Linton).
Cylindrophorus exceptus (Linton, 1924) Southwell, 1925.
Host: *Carcharinus leucas*, cub shark; Rockport, Tex. (Seamster).
Pedibothrium globicephalum Linton, 1909.
Host: *Ginglymostoma cirratum*, nurse shark; Dry Tortugas (Linton).
Pedibothrium longispine Linton, 1909.
Host: *Ginglymostoma cirratum*, nurse shark; Dry Tortugas (Linton).
Pedibothrium brevispine Linton, 1909.
Host: *Ginglymostoma cirratum*, nurse shark; Dry Tortugas (Linton).
Platybothrium hypoprioni Potter, 1937.
Host: *Negaprion brevirostris*, yellow shark; Dry Tortugas (Potter).
Onchobothrium sp. Linton, 1907.
Host: *Stoasodon narinari*, spotted sting ray; Dry Tortugas (Linton).

Family PROTEOCEPHALIDAE

Proteocephalus australis Chandler, 1935a.
Host: *Lepisosteus osseus*, long-nosed gar; Galveston Bay (Chandler).
Proteocephalus elongatus Chandler, 1935a.
Host: *Lepisosteus osseus*, long-nosed gar; Galveston Bay (Chandler).
Scolex pleuronectis Muller, 1788 (=*S. polymorphus* Rud., 1819, of many writers).

A larval form in intestine, cystic duct, or gall bladder of many teleost fishes including *Epinephelus striatus*, *Auxis thazard* (not a Gulf fish; probably *Euthynnus alletteratus*), *Mycteroperca bonaci*, *Lutjanus griseus*, and *Ocyurus chrysurus* at Dry Tortugas (Linton), and *Galeichthys felis* and *Bagre marina* from Galveston Bay (Chandler).

TRYPANORHYNCHA

Family TENTACULARIIDAE

Nybelinia palliata (Linton, 1924) Joyeux and Baer, 1936.
Host: *Sphyrna zygaena*, hammer-head shark; Englewood, Fla. (Chandler).

Family EUTETRARHYNCHIDAE

Eutetrarhynchus lineatus (Linton, 1909) Dollfus, 1942.
Host: *Ginglymostoma cirratum*, nurse shark; Dry Tortugas (Linton, Shuler).

Family OTOBOTHRIIDAE

Otobothrium penetrans Linton, 1907.
Hosts: *Carcharinus leucas*, cub shark; Dry Tortugas (Linton); *Carcharinus limbatus*, spot-fin ground shark; *Scoliodon terrae-novae*, sharp-nosed shark; Dry Tortugas (Shuler).
Otobothrium curtum (Linton, 1909) Dollfus, 1942.
Hosts: *Galeocerdo cuvier*, tiger shark; immature, *Mycteroperca bonaci*, black grouper; *Epinephelus striatus*, Nassau grouper; Dry Tortugas (Linton).
Otobothrium crenacolle Linton, 1890.
Host: *Carcharinus leucas*, cub shark; Dry Tortugas (Linton).
Poecilancistrium robustum (Chandler, 1935b) Dollfus, 1942.
Hosts: Im. *Cynoscion nebulosus*, spotted sea trout; Galveston Bay (Chandler); also abundant in *Pogonias cromis* on Texas coast (Chandler, unpublished).
Diploötobothrium springeri Chandler, 1942.
Host: *Sphyrna tudes*, hammer-head shark; Englewood, Fla. (Chandler).

Family DASYRHYNCHIDAE

Dasyrhynchus variouncinatus (Pintner, 1913) Pintner, 1928 (=*Tentacularia insignis* (Linton, 1924) Shuler, 1938; *Dasyrhynchus insigne* Chandler, 1942).
Host: *Negaprion brevirostris*, yellow shark; Dry Tortugas (Linton, Shuler).
Callitetrarhynchus gracilis (Rud., 1819) Dollfus, 1942 (=*Rhynchobothrium speciosum* Linton, 1897; *Tentacularia lepida* Chandler, 1935a; *Tentacularia pseudodera* Shuler, 1938).
Hosts: *Negaprion brevirostris*, yellow shark; Dry Tortugas (Shuler); Im., *Epinephelus straitus*, Nassau grouper, *Mycteroperca bonaci*, black grouper, *M. venenosa*, yellow-fin grouper, *Lutjanus griseus*, gray snapper; Dry Tortugas (Linton); *Galeichthys felis*, gaff-topsail catfish, *Bagre marina*, sea catfish; Galveston Bay (Chandler).

Family LACISTORHYNCHIDAE

Grillotia perelica (Shuler, 1938) Dollfus, 1942.
Host: *Negaprion brevirostris*, yellow shark; Dry Tortugas (Shuler).

Grillotia sp. (identified as *G. heptanchi* group by Dollfus).
Host: Im., *Cynoscion nebulosus*, Rockport, Tex. (unpublished).

Family PTEROBOTHRIIDAE

Pterobothrium heteracanthum Diesing, 1850 (=*Syndesmobothrium fillicolle* Linton, 1890; *Synbothrium fillicolle* Linton (1897); *Gymnorhynchus gigas* Chandler, 1935).
Hosts: *Dasyatis sabina*, southern sting ray; Dry Tortugas (Linton); Im., *Calamus calamus*, saucer-eye porgy; Dry Tortugas (Linton); *Galeichthys felis*, gaff-topsail catfish, *Micropogon undulatus*, croaker; Galveston Bay (Chandler).

Pterobothrium lintoni (MacCallum, 1916) Dollfus, 1942 (=*Tetrarhynchus erinaceus* Linton, 1897; *Gymnorhynchus malleus* (Linton, 1924; Chandler, 1935).
Host: Im., *Galeichthys felis*, gaff-topsail catfish; Galveston Bay (Chandler).

Incertae Sedis

Rhynchobothrium simile Linton, 1909 (possibly a Lacistorhynchus according to Dollfus, 1942).
Host: *Ginglymostoma cirratum*, nurse shark; Dry Tortugas (Linton).

Rhynchobothrium tenuispine Linton, 1890.
Host: *Ginglymostoma cirratum*, nurse shark; Dry Tortugas (Linton).

Rhynchobothrium binuncum Linton, 1909.
Host: *Dasyatis sabina*, southern sting ray; Dry Tortugas (Linton).

Rhynchobothrium exile Linton, 1909 (probably a Callitetrarhynchus according to Pintner, 1931; Dollfus disagrees).
Host: *Galeocerdo cuvier*, tiger shark; Dry Tortugas (Linton). In addition, various unidentified species of Rhynchobothrium, both adults and larvae, were reported from various fishes from Dry Tortugas by Linton (1909). Perez Vigueras reported three species of larval Trypanorhyncha from marine teleosts off Havana, Cuba, and Seamster (personal communication) reported a "Tetrarhynchus sp." from *Carcharinus leucas* off Rockport, Tex.

PSEUDOPHYLLIDEA

Family PTYCHOBOTHRIIDAE

Ptychobothrium belones (Duj., 1845) Lönnberg, 1869 (=*Dibothrium restiforme* Linton, 1891).
Hosts: *Strongylura notata*, needlefish, *S. rhaphidoma*, houndfish; Dry Tortugas (Shuler).

Clestobothrium crassiceps (Rud., 1819) Lühe, 1899.
Hosts: *Merluccius bilincaris*, silver hake, *Chlorophthalmus truculentus*, green-eye, *Merluccius* sp.; Dry Tortugas (Shuler).

Bothriocephalus sp. (Linton, 1908) (=*Dibothrium* sp., Linton, 1908).
Host: Im., *Hepsetia stipes*, silverside; Dry Tortugas (Linton).

CYCLOPHYLLIDEA

Incertae Sedis

Glossocercus cyprinodontis Chandler, 1935 (probably Dilepididae).
Host: Im., *Cyprinodon variegatus;* Galveston Bay (Chandler).

Cysticercoides menidiae Chandler, 1935.
Host: Im., *Menidia berrylina peninsulae*, silversides; Galveston Bay (Chandler).

NOTE.—Bibliography follows chapter on Nematoda, p. 358.

ACANTHOCEPHALA

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In contrast to the trematodes and cestodes, very few species of Acanthocephala have been reported from Gulf animals. To some extent, certainly, this is due to the scantiness of investigations, particularly on parasites of fishes of bays and estuaries, but enough work has been done to make it evident that the Acanthocephala are not as abundant in the Gulf as they are in more northern waters, e. g., Woods Hole, Massachusetts. Linton (1907) called attention to this relative scarcity of Acanthocephala, both of species and of individuals, in southern seas, for he observed it not only at Dry Tortugas in the Gulf but also at Beaufort, North Carolina, and at Bermuda. In a later collection at Dry Tortugas (Linton 1909) he remarked that Acanthocephala were found in only 7 of the 32 species of fish examined, and in every case few or even only 1 was found, all belonging to a single species which he called *Echinorhynchus pristis*, now known as *Nipporhynchus ornatus*. In a personal communication Seamster (1950) reported only 1 specimen of 30 fish examined in Corpus Christi Bay, Texas, representing 16 species, to harbor an acanthocephalan. Chandler (1935a), on the other hand, in an examination of 23 species of teleost fish from Galveston Bay represented by from 1 to over 100 specimens of each found a predominance of Acanthocephala as common adult parasites. However, no elasmobranchs were examined so the varied tetraphyllidean and trypanorhynchan cestodes found practically universally in the spiral valves of these hosts did not come into the picture. The three adult species of Acanthocephala found were all fairly common in their respective hosts and were the only adult parasites that one could depend on finding in repeated examinations of particular hosts. Acanthocephala will probably be found to be fairly common in fishes frequenting the shores and shallow bays throughout the Gulf where small Crustacea, which probably serve as intermediate hosts, abound; but they will probably not be found abundantly in oceanic or reef-dwelling fishes.

EOACANTHOCEPHALA

Family NEOECHINORHYNCHIDAE

Atactorhynchus verecundus Chandler, 1935a
Host: *Cyprinodon variegatus;* Galveston Bay (Chandler)

PALAEACANTHOCEPHALA

Family GORGORHYNCHIDAE

Gorgorhynchus gibber Chandler, 1934
Host: *Galeichthys felis*, gaff-topsail catfish; Galveston Bay (Chandler)

Nippostrongylus ornatus (Van Cleave, 1918) Van Cleave and Lincicome, 1940 (=*Rhadinorhynchus pristis* (Rud., 1802) of Linton, 1891–1909)
Hosts: *Auxis thazard* (*Euthynnus alletteratus*?), frigate mackerel, *Haemulon sciurus*, yellow grunt, *Haemulon plumieri*, white grunt, *Lutjanus griseus*, gray snapper, and four other species, unnamed; Dry Tortugas (Linton)

Filisoma fidum Van Cleave and Manter, 1947
Host: *Kyphosus sectatrix*, rudder fish; Dry Tortugas (Van Cleave and Manter)

Family RHADINORHYNCHIDAE

Illiosentis furcatus Van Cleave and Lincicome, 1939
Host: *Menticirrhus americanus*, southern kingfish; Grand Isle, La. (Van Cleave and Lincicome), Corpus Christi Bay, Tex. (Seamster)

Telosentis tenuicornis (Linton, 1891) Van Cleave, 1947
Hosts: *Micropogon undulatus*, croaker, *Leiostomus xanthurus*, spot; Galveston Bay (Chandler)

Family CENTRORHYNCHIDAE

Arhythmorhynchus duocinctus Chandler, 1935a
Host: Im., *Paralichthys lethostigmus*, southern flounder; Galveston Bay (Chandler)

NOTE.—Bibliography follows chapter on Nematoda, p. 358

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NEMATODA

By ASA C. CHANDLER, *Rice Institute*

Remarkably few nematodes, either adults or larvae, have been identified in fishes or other animals of the Gulf. The only work done on them known to the writer is Linton's work at Dry Tortugas (1907–1909) and my own work on fishes of Galveston Bay (1935a). In addition, a single species of oxyurid, *Laurotravassoxyuris travassosi*, was described by Perez Vigueras (1938) from a teleost on the north coast of Cuba.

Linton called attention to the fact that nematodes were sparingly represented, as were Acanthocephala, in the fishes he examined at Dry Tortugas as compared with the large numbers, particularly of encysted immature forms, in fishes at Woods Hole, Massachusetts. In the Gulf fishes immature encysted forms were found in only 7 of 32 species examined and in small numbers in all except the yellow-fin grouper, *Mycteroperca venenosa*, whereas in the north such nematodes were found in the viscera of a large number of species of fishes, often in great numbers. Linton found adult nematodes in only 6 species of fish, "(1 elasmobranch and 5 teleosts)" but except for the species found in the stomach of a nurse shark only 1 or 2 specimens were found in a host.

Chandler found nematodes, like Acanthocephala, to be relatively more frequent in the inshore fishes of Galveston Bay than in the oceanic and reef fishes examined by Linton, but they could certainly not be considered abundant, either in species or individuals. In 23 species of teleosts studied 3 adult nematodes were found, each represented by only 1 or 2 specimens in single host individuals. Nine species of immature nematodes were found, but only two, both belonging to the genus *Contracaecum*, occurred frequently in their particular hosts and then in only moderate numbers. Seamster (1950), in a personal communication, reported finding 1 nematode infestation in 30 fish belonging to 16 genera from Corpus Christi Bay; this nematode was not identified.

Most of the nematodes found by Linton have been inadequately described and have not been given specific names. The larval forms found by Chandler were all described as fully as the material available would permit and were all tentatively designated new species until the adults become known.

ASCARIDATA

Family OXYURIDAE

Laurotravassoxyuris travassosi Perez Vigueras, 1938.
Host: *Holacanthus tricolor*, rock beauty; Havana (Perez Vigueras).

Family ASCARIDIDAE

Acanthocheilus sp. Linton, 1909.
Host: *Ginglymostoma cirratum*, nurse shark; Dry Tortugas (Linton).

Amphicaecum parvum Chandler, 1935a.
Host: Im., *Dorosoma cepedianum*, gizzard shad; Galveston Bay (Chandler).

Contracaecum chaunaxi Olsen, 1952.
Host: *Chaunax* sp.; Dry Tortugas (Olsen).

Contracaecum collieri Chandler, 1935a.
Hosts: Im., *Cyprinodon variegatus*, broad killifish, *Paralichthys lethostigmus*, southern flounder; Galveston Bay (Chandler).

Contracaecum histiophori Yamaguti, 1935.
Host: *Istiophorus americanus;* Florida coast (Olsen).

Contracaecum ogcocephali Olsen, 1952.
Host: *Ogcocephalus radiatus;* Dry Tortugas (Olsen).

Contracaecum robustum Chandler, 1935a.
Hosts: Im., *Mugil cephalus*, mullet, *Fundulus* sp. (probably *grandis*), common killifish; Galveston Bay (Chandler).

Goezia minuta Chandler, 1935a.
Host: *Bagre marina*, sea catfish; Galveston Bay (Chandler).

Heterotyphlum eurycheilum Olsen, 1952.
Host: *Promicrops itaiara;* Dry Tortugas (Olsen).

Rhaphidascaris anchoviellae Chandler, 1935a.
Hosts: Im., *Anchoa epsetus*, striped anchovy, *Menidia berrylina peninsulae*, silversides; Galveston Bay (Chandler). Immature ascarids in small numbers recorded by Linton (1907) from the following hosts at Dry Tortugas: *Sphyraena barracuda, Haemulon sciurus, H. flavolineatum, H. macrostomum, Mycteroperca bonaci, M. venenosa, Ocyurus chrysurus, Epinephelus striatus,* and *Hepsetia stipes.*

Rhaphidascaris lutiani Olsen, 1952.
Host: *Lutianus analis;* Dry Tortugas (Olsen).
Terranova ginglymostomae Olsen, 1952.
Host: *Gingylostoma cirratum;* Dry Tortugas (Olsen).
Terranova secundum (Chandler, 1935) Olsen, 1952.
Host: Im., *Trichiurus lepturus*, cutlass fish; Galveston Bay (Chandler).
Terranova trichiuri (Chandler, 1935) Olsen, 1952.
Host: Im., *Trichiurus lepturus*, cutlass fish; Galveston Bay (Chandler).

Family CUCULLANIDAE

Dichelyne fastigatus Chandler, 1935a.
Host: *Sciaenops ocellatus*, redfish; Galveston Bay (Chandler).
Dichelyne diplocaecum Chandler, 1935a.
Host: *Ictalurus furcatus*, channel cat, usually found in fresh water, Galveston Bay (Chandler).

Family PHILOMETRIDAE

Philometra sp. (Linton, 1907) (=*Ichthyonema* sp. Linton, 1907).
Hosts: *Lutjanus griseus*, gray snapper, *Strongylura marina*, billfish; Dry Tortugas (Linton).

Incertae Sedis

Agamonema immanis Chandler, 1935a (possibly a *Philometra*).
Hosts: *Fundulus* sp. (*grandis?*), *Cyprinodon variegatus*, killifishes; Galveston Bay (Chandler).
Agamonema vomitor Chandler, 1935a.
Host: *Ictalurus furcatus*, channel cat (usually found in fresh water); Galveston Bay (Chandler).

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CHAPTER XI

BRYOZOA, BRACHIOPODA, PHORONIDA, AND ENTEROPNEUSTA

THE BRYOZOA OF THE GULF OF MEXICO

By RAYMOND C. OSBURN, *Allan Hancock Foundation, University of Southern California*

Bryozoans are abundant organisms everywhere in the seas, from the polar regions to the tropics, from the shore line to great depths, but with only a few representatives in fresh water. The individuals are all small, rarely more than one millimeter in length, but their capacity for budding is so great that they often produce colonies of considerable size. With a few exceptions the colonies are all attached, and most of them are encrusting. Some species produce thick nodular masses by the piling up of layer on layer, while still others grow erect in branching bushy colonies to the height of several inches. Within the Gulf, they are abundant, encrusting shells, stones, dead corals and corallines, algae, or anything else that may afford attachment. The individuals are encased in hard chitinous or calcareous walls, and they appear to be of little importance in the food chain of other animals, but their nuisance value in the fouling of ship bottoms and buoys and the covering of oyster beds to the exclusion of young oysters is of considerable economic importance. The rate of budding is so rapid that oyster shells used as cultch on oyster beds may be completely covered in a few weeks to the exclusion of oyster larvae.

Apparently the first mention of Bryozoa from the Gulf is the small list of 7 species by Count de Pourtalès in 1867. Pourtalès then turned the material obtained by him on the expeditions of the U. S. Coast Survey, 1867 to 1869, over to the Swedish zoologist Smitt for further study. The area concerned was that about the Tortugas Islands and the Straits of Florida, and Smitt reported on 95 species, many of them new. In 1914, Osburn discussed 83 species obtained by him in shallow water around the Tortugas Islands, adding 40 species to Smitt's list. In 1928, Canu and Bassler reported on more than 40 dredgings made by the U. S. Fisheries Steamer *Albatross* and added 36 more species, most of them new to the Bryozoa of the Gulf. This makes a total of only about 170 species known from this great area, depending more or less on just where the boundary line is drawn and also on the indefinite nature of some of Smitt's records.

From the neighboring West Indian and Caribbean waters, Busk (1884) listed 5 species from near Puerto Rico, and in 1909, Levinsen mentioned a few species from the Virgin Islands. Osburn (1927) reported on a small collection of 23 species taken by Dr. C. J. van der Horst at Curaçao Island; in 1940, on his own collection of 124 species from the southern shores of Puerto Rico; and in 1947, on 107 species recovered by the Allan Hancock Atlantic Expedition off the southern shores of the Caribbean Sea. All of these reports will be useful in the study of the Bryozoa of the Gulf. The reports by Canu and Bassler (1928) and Osburn (1940) contain descriptions and references for all of the Gulf species.

The Bryozoa of this region are strictly warm-water species, many of them known to be circumtropical in distribution, and of the 170 species recorded, 105 have a wide range in other seas. Only 35 have not been recorded outside of the Gulf, and some of these will undoubtedly be found elsewhere.

It might be supposed that the Gulf species would show a close relationship to those of the Pacific across the narrow region of Central America, but such is not the case. It is true that 93 of the 170 Gulf species occur also in the eastern Pacific, but nearly all of these are species of wide distribution, and only 16 have been found only in the Gulf and the near waters of the Pacific. It would appear that most of the species have been evolved since the waters of the Atlantic were last closed off from the Pacific.

In the different groups of Bryozoa the numbers of known species are as follows:

Cyclostomata: 8 species recorded from within the Gulf and 10 more from the adjoining West Indian region; many more undoubtedly occur.

Ctenostomata: only 5 species within the Gulf and 8 more in the West Indian area, but the only references to this group are those of Osburn, 1914, from the Tortugas, and 1940, from Puerto Rico.

Cheilostomata: about 155 species within the Gulf with many more from around the West Indian Islands and the Caribbean Sea.

Very little of the great area of the Gulf has been explored biologically, and our knowledge of the fauna is limited almost entirely to that of the coastal shelf reaching from the Straits of Florida to the Mississippi Delta. Here the dredgings have practically all been above the 100-fathom line. Intensive collection has been done in only a few places; for the Bryozoa, only around the Tortugas Islands. In all of the western part of the Gulf and around to Yucatán even the shallow waters are untouched, the deeper waters are also unknown territory, and careful collecting from the shore lines to the abyssal regions will undoubtedly yield a wealth of information.

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BRACHIOPODA OCCURRING IN THE GULF OF MEXICO

By G. ARTHUR COOPER, *Curator, Invertebrate Paleontology and Paleobotany, U. S. National Museum*

Brachiopods are rare or uncommon animals in most parts of the modern world. They occur in abundance in a few places only, such as off southern Australia, New Zealand, and parts of Japan. They occur in lesser variety in the northern Atlantic, the Arctic, Antarctic, and Mediterranean. They are thus worldwide in distribution. Although rare at the present time, brachiopods were abundant in the past. Paleozoic seas abounded in brachiopods, but in the Mesozoic era, although numerous, they began to lose ground to the Mollusca. Furthermore, in the Mesozoic era their family representation became reduced; this was the great time for the Rhynchonellacea and was the time of upsurge of the Terebratulacea, or looped forms.

Following the Mesozoic era, Tertiary time saw a further reduction of brachiopods as the Mollusca continued to expand. Tertiary brachiopods are generally not abundant, but areas where they are common are New Zealand, southern Australia, and Japan. They are also fairly common in the Mediterranean and West Indies regions. It is interesting to note that these areas of abundance correspond closely with modern distribution. Recent brachiopods are similar to Tertiary ones, and their roots can be satisfactorily traced into the Tertiary and on into the Mesozoic in several instances.

The brachiopods found so far in the Gulf of Mexico are mostly types inherited from the Tertiary of the Middle Atlantic and West Indian regions. The latter influence is very strong, and most of the Gulf species are the same as those occurring in the waters around the West Indies. These Gulf species are *Glottidia pyramidata* (Stimpson), *Crania pourtalesii* Dall, *Cryptopora gnomon* Jeffreys, *Chlidonophora incerta* (Davidson), *Terebratulina cailleti* Crosse, *Gryphus cubensis* (Pourtalès), *G. bartschi* Cooper, *G. bartlettii* (Dall), *Argyrotheca barrettiana* (Davidson), *A. lutea* (Dall), *A. schrammi* (Crosse and Fischer), *Dallina floridana* (Pourtalès).

The species recorded from the Gulf, except for *Glottidia*, occur in West Indian waters. A number of brachiopods that have West Indian affinities are also known from the south side of the Florida Keys. Both of these areas have yielded species not yet recorded from Gulf waters, but any of these species may yet be found in the Gulf with more intensive searching. These are *Thecidellina barretti* (Davidson) 1866, *Eucalathis* n. sp., *Platidia seminula* (Philippi) 1836, and *Pantellaria echinata* (Fischer and Oehlert).

The information recorded in this paper was derived from the records published by W. H. Dall supplemented by data with specimens in the national collection of Recent brachiopods. Dall's Annotated List of the Recent Brachiopods in the Collection of the United States National Museum, with Description of Thirty-three New Forms gives data for most occurrences up to 1920. Unfortunately, several of the Gulf species in the national collections have no bathymetric data, and several have no geographic information other than their origin in the Gulf. I am indebted to Dr. Harry B. Whittington, Harvard University, for additional data on Gulf brachiopods in the collections of the Museum of Comparative Zoology, Harvard University.

Glottidea pyramidata (Stimpson)

Lingula pyramidata Stimpson. Am. Jour. Sci., ser. 2, vol. 29, 1860, p. 444.

This species has the characteristic form of the familiar *Lingula*, but it is small, about 15 millimeters long and has a pale yellow or light brown color. It has been taken from Tampa Bay, Cedar Keys, and Marco on the Gulf coast of Florida. The specimens from Marco are from 1 to 3 fathoms. Like *Lingula*, this genus is a shallow-water dweller.

Crania pourtalesii Dall

Crania anomala var. *pourtalesii* Dall. Bull. Mus. Comp. Zool., Harvard, vol. 3, 1871, p. 35, pl. 1, figs. 7a-b.

Crania is rare in North American waters, and only a few specimens of this species are known. It forms a low cone attached to corals or masses of rock. The color is pale yellow, and the shell measures about 8 millimeters. A specimen from Campeche Bank, latitude 23°18′, longitude 87°02′, is the only one from the Gulf.

Cryptopora gnomon Jeffreys

Cryptopora gnomon Jeffreys. Nature, Dec. 2, 1869, p. 136.

This is the only member of the Rhynchonellacea known from the Gulf of Mexico. It can be recognized by its small size (2 to 3 mm. long), rounded triangular outline, sharply pointed beak, and glossy, translucent shell. The interior of the brachial valve has a high median septum. It occurs off Cape San Blas in gray mud at 196 fathoms; also, at 210 fathoms off the Mississippi River.

Chlidonophora incerta (Davidson)

Megerlia ? incerta, n. sp., Davidson. Proc. Roy. Soc., vol. 27, 1878, p. 438.

This shell may be recognized by its nearly circular form, nearly white color, and finely ribbed surface. It has an unusually long pedicle with frayed end. Inside the brachial valve the loop forms an incomplete ring. The species is a deep-water form in most of its known occurrences. It was taken at 1,181 fathoms in the Gulf between the delta of the Mississippi River and Cedar Key.

Terebratulina cailleti Crosse

Terebratulino eailleti Crosse. Jour. Conchyl., vol. 13, 1865, p. 27, pl. 1, figs. 1–3.

Small, oval, pale yellow in color, and finely ribbed are features characterizing this species. The ribbing at the beak and umbo is somewhat beaded. The interior of the brachial valve is provided with a stout loop in the form of a ring attached to two short descending branches. It was taken in 399 fathoms off Arrowsmith Bank, Yucatán; also, 640 fathoms in Yucatán Strait.

Gryphus cubensis (Pourtalès)

Terebratula cubensis Pourtalès. Bull. Mus. Comp. Zool., Harvard, vol. 1, No. 6, 1867, p. 109.

This is a large brachiopod which attains a length of over 45 millimeters. It is generally yellowish in color and has a somewhat triangular outline. The anterior margin is rectimarginate. The brachial valve has a short loop consisting of two descending lamellae and a narrow connecting band. Taken at 119 fathoms, latitude 26°31′, longitude 85°03′ (Harvard collection). National Museum specimens without specific data.

Gryphus bartschi Cooper

Gryphus bartschi Cooper. Smithsonian Misc. Coll., vol. 91, No. 10, 1934, pl. 1, figs. 1–8.

This species is smaller than *G. cubensis* (Pourtalès), has a smaller foramen, and is less triangular in outline. It is of an orange-yellow color. It is from Bay of Florida and was taken at 101 fathoms.

Gryphus bartlettii (Dall)

Terebratula bartlettii Dall. Amer. Naturalist, vol. 16, 1882, p. 885.

Large size, white or salmon color, and a strongly and broadly plicated anterior commissure distinguish this species from the others. No definite locality in the Gulf is recorded by Dall.

Argyrotheca barrettiana (Davidson)

Argiope barrettiana Davidson. Proc. Zool. Soc., Feb. 1866, p. 103, pl. 12, fig. 3.

This is a small brachiopod (about 9 mm. wide) but an unusually beautiful species. It is somewhat rectangular in outline, wider than long, and with 20 strong, rounded radial costae. Most distinctive of the species is its coloration. The elevated costae are pale, straw-yellow, but the interspaces are crimson. It has been taken at 101 fathoms in the Gulf but the exact locality not recorded.

Argyrotheca lutea (Dall)

Cistella lutea Dall. Bull. Mus. Comp. Zool., Harvard, vol. 3, 1871, p. 20, pl. 1, figs. 5, 5a; pl. 2, figs. 4–8.

This species is somewhat less transverse than the preceding and differs in its straw-yellow color. It has been taken from 30–40 fathoms off Tortugas.

Argyrotheca schrammi (Crosse and Fischer)

Argiope schrammi Crosse and Fischer. Jour. Conchyl., vol. 14, 1866, p. 269, pl. 8, fig. 6.

Argyrotheca schrammi is a small species (about 5 mm. wide) with about 10 strong, rounded costae which are opposite on each valve, thus forming a scalloped edge. Specimens may be uniformly red but also may be marked like *A. barrettiana*. Ones so marked are termed *A. schrammi rubrotincta* (Dall). The species is reported from off Tortugas

and Yucatán Strait at 540 fathoms (Harvard collection).

***Dallina floridana* (Pourtalès)**

Waldheimia floridana Pourtalès. Bull. Mus. Comp. Zool., Harvard, vol. 1, 1868, p. 127.

This is a large (20 mm. long), yellow species having a strongly triangular outline and a deep fold in the anterior commissure. The loop is long, broad, and complicated. The National Museum specimens have no other data than Gulf of Mexico.

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PHORONIDA

By Joel W. Hedgpeth, *Scripps Institution of Oceanography, University of California*

There seems to be no record of adult phoronids in the Gulf of Mexico, hence it is not possible to identify the species represented by the actinotroch larvae which occur during the winter months in the neritic waters of the Gulf of Mexico. These larvae have been seen in plankton tows in Louisiana bays and have at times been common in tows taken from the dock in the ship channel at Port Aransas. Some larvae have been carried through metamorphosis to the juvenile phoronid stage, but this is still too immature to identify them even to genus. While it would not be surprising to find that the same species known to occur in the Beaufort area also occurs on the Gulf coast, this is not adequate for assigning a name to the actinotroch larva of the Gulf coast. The Beaufort species, together with additional larvae, is described by Brooks and Cowles (1905). Recently, Marcus (1949) has described the morphology and embryology of a form in Santos, Brazil, which she identifies with the north European *Phoronis ovalis*. This species is reported to live in burrows in shells of *Thais floridana*. While phoronids have not been observed in this situation on the Gulf coast, this Brazilian record suggests an intensive search might be profitable.

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ENTEROPNEUSTA

By JOEL W. HEDGPETH, *Scripps Institution of Oceanography, University of California*

The balanoglossids of the Gulf of Mexico are incompletely known; determination of various finds in coastal waters are contingent upon revisionary work in the genera concerned. A large species of *Balanoglossus*, some specimens exceeding 50 centimeters in length, is common in the vicinity of Englewood, Florida. A similar, if not identical, species occurs in the Grand Isle region, especially near the eastern end of the island in the mud flats. A small acorn worm, belonging to the genus *Saccoglossus*, occurs in the clean sand flats at Rockport, Texas. Found at Dry Tortugas, and to be expected elsewhere in the Gulf in coarse coral sand, is *Ptychodera bahamensis*, a species occurring generally in the Caribbean region.

CHAPTER XII
ECHINODERMS

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ECHINODERMS (OTHER THAN HOLOTHURIANS) OF THE GULF OF MEXICO

By AUSTIN H. CLARK, *U. S. National Museum*

The first definite record of an echinoderm from the Gulf of Mexico was published in 1758 when Albertus Seba described and figured *Stella marina polyactis* seu *Luna marina* (*Nemaster grandis*) from New Spain, presumably the eastern coast of Mexico. From time to time scattered notices of other species appeared, mostly from Mexico.

In 1867 investigation of the sea bottom in deep water was undertaken by the United States Coast Survey in the steamer *Corwin* under the direction of Count L. F. de Pourtalès. Four dredge hauls were made in from 96 to 350 fathoms off the Florida Keys and northern Cuba. In 1869 the U. S. C. S. S. *Bibb* made a number of deep hauls about the Florida Keys and off northern Cuba. In 1872 the *Bibb* dredged in from 17 to 1,164 fathoms in the Yucatán Channel and on the Yucatán Bank, with a few hauls among the Florida Keys, and in the same year the *Blake* made many dredge hauls about the Keys and off the west coast of Florida.

In 1877–78 the *Blake*, under the direction of Alexander Agassiz, continued work about the Florida Keys, north of Havana, and on and about the Yucatán Bank, with a few hauls off the mouth of the Mississippi. In 1880 the *Blake* made a single dredge haul east of Cape Catoche, Yucatán.

In 1884, 1885, and 1886 the U. S. Fish Commission steamer *Albatross* took a number of dredge hauls off Havana and in the Gulf of Mexico. Subsequently, the Bureau of Fisheries ships *Fish Hawk* and *Grampus* worked along the west coast of Florida.

The Bahama Expedition of the State University of Iowa made a few dredge hauls off Havana in 1893, and in 1938 and 1939 the *Atlantis* of the Woods Hole Oceanographic Institution made an intensive survey of the deeper waters about Cuba.

John B. Henderson, in his yacht *Eolis*, dredged extensively about the Florida Keys and on the Pourtalès Plateau, and Hubert Lyman Clark made intensive studies of the littoral species at Tortugas under the auspices of the Department of Marine Biology of the Carnegie Institution of Washington. Waldo L. Schmitt also collected much interesting material in the same region.

It is most gratifying to be able to say that all the echinoderms from these collections, both governmental and private, have been studied and reports on them published. Furthermore, the material has been collected in comprehensive monographs by Mortensen (Echinoidea), H. L. Clark (Ophiuroidea), Döderlein (Euryalidae and Gorgonocephalidae), and A. H. Clark (Crinoidea), so that the relationships of the various species to others in different parts of the world may be readily appreciated.

But it is evident that by far the greatest part of our knowledge of the echinoderms of the Gulf of Mexico is confined to those species in the extreme southeast, about the Florida Keys and along the northern coast of Cuba. The remainder of the Gulf is largely a blank, and this is especially true of the zone between the shore line and 150 fathoms where undoubtedly many additional species remain to be discovered. Even among the Florida Keys, the most thoroughly worked of any comparable warm water area, there is still much to be found as is evident from the recent discovery of such conspicuous shallow water species as *Astropyga magnifica*, *Copidaster lymani*, *Ophidiaster bayeri*, and *Schizostella bifurcata* .

CRINOIDEA

Family COMASTERIDAE

Nemaster grandis A. H. Clark.
Nemaster iowensis (Springer).
Nemaster rubiginosa (Pourtalès).
Nemaster discoidea (P. H. Carpenter).
Neocomatella pulchella (Pourtalès).
Neocomatella alata (Pourtalès).
Leptonemaster venustus A. H. Clark.
Comatonia cristata (Hartlaub).
Comaetinia echinoptera (J. Müller).

Family COLOBOMETRIDAE

Analcidometra armata (Pourtalès).

Family THALASSOMETRIDAE

Stylometra spinifera (P. H. Carpenter).
Horaeometra duplex (P. H. Carpenter).

Family CHARITOMETRIDAE

Crinometra brevipinna (Pourtalès).
Crinometra brevipinna var. *insculpta* A. H. Clark.
Crinometra brevipinna var. *concinna* A. H. Clark.
Crinometra brevipinna var. *margaritacea* A. H. Clark.
Crinometra brevipinna var. *diadema* (Hartlaub).
Crinometra brevipinna var. *brevipinna* (Pourtalès).
Crinometra brevipinna var. *gemmata* A. H. Clark.
Crinometra brevipinna var. *granulosa* (Hartlaub).
Crinometra brevipinna var. *granulifera* (Pourtalès).
Crinometra brevipinna var. *pulchra* A. H. Clark.

Family ANTEDONIDAE

Compsometra nuttingi A. H. Clark.
Coccometra hagenii (Pourtalès).
Coccometra nigrolineata A. H. Clark.
Coccometra guttata A. H. Clark.
Hypalometra defecta (P. H. Carpenter).
Zenometra columnaris (P. H. Carpenter).
Caryometra monilicirra A. H. Clark.
Caryometra atlantidis A. H. Clark.
Caryometra tenuipes (A. H. Clark).
Caryometra spinosa A. H. Clark.
Caryometra lisa A. H. Clark.
Caryometra alope A. H. Clark.
Trichometra cubensis (Pourtalès).

Family ATELECRINIDAE

Atelecrinus balanoides P. H. Carpenter.

Family ISOCRINIDAE

Cenocrinus asteria (Linné).
Neocrinus decorus Wyville Thomson.
Neocrinus blakei (P. H. Carpenter).
Endoxocrinus parrae (Gervais).
Endoxocrinus prionodes H. L. Clark.
Diplocrinus carolinae A. H. Clark.

Family HOLOPIDAE

Holopus rangii d'Orbigny.

Family BATHYCRINIDAE

Monachocrinus caribbeus (A. H. Clark).
Rhizocrinus lofotensis M. Sars.
Democrinus robustus (A. H. Clark).
Democrinus rawsonii (Pourtalès).[1]

ECHINOIDEA

Family CIDARIDAE

Histocidaris sharreri (A. Agassiz).
Histocidaris nuttingi Mortensen.
Stereocidaris ingolfiana Mortensen.
Cidaris abyssicola (A. Agassiz).
Cidaris rugosa (H. L. Clark).
Cidaris blakei (A. Agassiz).
Calocidaris micans (Mortensen).
Stylocidaris affinis (Philippi).
Eucidaris tribuloides (Lamarck).

Family ECHINOTHURIDAE

Phormosoma placenta Wyville Thomson.
Hygrosoma petersii (A. Agassiz).
Araeosoma fenestratum (Wyville Thomson).
Araeosoma belli Mortensen.[2]

Family SALENIIDAE

Salenocidaris varispina A. Agassiz.
Salenia goësiana Lovén.

Family ARBACIDAE

Habrocidaris scutata (A. Agassiz).
Podocidaris sculpta (A. Agassiz).
Arbacia punctulata (Lamarck).
Coelopleurus floridanus A. Agassiz.

Family ASPIDODIADEMATIDAE

Plesiodiadema microtuberculatum (A. Agassiz).
Plesiodiadema antillarum (A. Agassiz).
Aspidodiadema jacobyi A. Agassiz.

Family DIADEMATIDAE

Astropyga magnifica A. H. Clark.
Diadema antillarum (Philippi).
Centrostephanus rubricingulus H. L. Clark.

Family TEMNOPLEURIDAE

Trigonocidaris albida A. Agassiz.
Genocidaris maculata A. Agassiz.

Family TOXOPNEUSTIDAE

Lytechinus variegatus (Lamarck).
Lytechinus variegatus var. *variegatus* Lamarck.
Lytechinus variegatus var. *carolina* A. Agassiz.
Tripneustes ventricosus (Lamarck).

Family ECHINIDAE

Echinus gracilis A. Agassiz.

Family ECHINOMETRIDAE

Echinometra lucunter (Linné).[3]
Echinometra viridis A. Agassiz.

Family ECHINONEIDAE

Echinoneus cyclostomus Leske.

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[1] An undersea photograph taken by D. M. Owen, Woods Hole Oceanographic Laboratory, in lat. 27°18′ N., long. 85°30′ W., west of Florida, in 1,200 fathoms, shows a 10-armed stalked crinoid that may be *Bathycrinus aldrichianus* Wyville Thomson. See Science News Letter, vol. 60, No. 15, October 13, 1951, p. 227.

[2] Mortensen gives *Tromikosoma hispidum* from the Gulf of Mexico by error for the Gulf of California.

[3] In the western part of the Gulf of Mexico this species is frequently circular, and is then easily mistaken for a species of *Heliocidaris*. Verrill in 1867 recorded (?) *Anthocidaris mexicana* A. Ag. from Vera Cruz. In the reprint of his article he says that Mr. Agassiz considers this his *Echinometra plana* (= *E. viridis*). It is probably the circular variety of *E. lucunter*.

Family ECHINOLAMPADIDAE

Echinolampas depressa Gray.
Conolampas sigsbei (A. Agassiz).

Family NEOLAMPADIDAE

Neolampas rostellata A. Agassiz.

Family CLYPEASTRIDAE

Clypeaster rosaceus (Linné).
Clypeaster euclastus H. L. Clark.
Clypeaster cyclopilus H. L. Clark.
Clypeaster ravenelii (A. Agassiz).
Clypeaster prostratus (Ravenel).

Family FIBULARIIDAE

Echinocyamus grandiporus Mortensen.
Echinocyamus macrostomus Mortensen.

Family SCUTELLIDAE

Mellita quinquiesperforata (Leske).
Mellita quinquiesperforata var. *quinquiesperforata* (Leske).
Mellita quinquiesperforata var. *tenuis* H. L. Clark.
Mellita quinquiesperforata var. *lata* H. L. Clark.
Mellita sexiesperforata (Leske).
Encope michelini L. Agassiz.

Family POURTALESIIDAE

Pourtalesia miranda A. Agassiz.

Family PALAEOPNEUSTIDAE

Palaeopneustes cristatus A. Agassiz.
Archaeopneustes hystrix (A. Agassiz).
Linopneustes longispinus (A. Agassiz).
Homolampas fragilis (A. Agassiz).
Palaeotropus josephinae Lovén.

Family AEROPSIDAE

Aceste bellidifera Wyville Thomson.

Family HEMIASTERIDAE

Hemiaster expergitus Lovén.

Family LOVENIIDAE

Echinocardium laevigaster A. Agassiz.

Family SCHIZASTERIDAE

Schizaster orbignyanus A. Agassiz.
Hypselaster limicolus (A. Agassiz).
Moira atropos (Lamarck).
Agassizia excentrica A. Agassiz.

Family BRISSIDAE

Neopneustes micrasteroides (A. Agassiz).
Brissopsis alta Mortensen.
Brissopsis atlantica Mortensen.
Plethotaenia spatangoides (A. Agassiz).
Plagiobrissus grandis (Gmelin).
Brissus unicolor (Leske).
Meoma ventricosa (Lamarck).

ASTEROIDEA

Family GONIOPECTINIDAE

Goniopecten demonstrans Perrier.
Prionaster elegans Perrier.

Family ASTROPECTINIDAE

Astropecten articulatus (Say).
Astropecten articulatus var. *articulatus* (Say).
Astropecten articulatus var. *valenciennesi* Müller and Troschel.
Astropecten cingulatus Sladen.
Psilaster squameus H. L. Clark.
Plutonaster bifrons (Wyville Thomson).
Plutonaster intermedius (Perrier).
Persephonaster pulcher (Perrier).
Persephonaster echinulatus H. L. Clark.
Persephonaster spinulosus H. L. Clark.
Tethyaster grandis (Verrill).
Tethyaster vestita (Say).[4]

Family LUIDIIDAE

Luidia senegalensis Müller and Troschel.
Luidia barbadensis Perrier.
Luidia variegata Perrier.
Luidia convexiuscula Perrier.
Luidia alternata (Say).
Luidia clathrata (Say).[5]

Family BENTHOPECTINIDAE

Benthopecten spinosus Verrill.
Cheiraster coronatus (Perrier).
Cheiraster mirabilis (Perrier).
Luidiaster mixtus (Verrill).

Family ODONTASTERIDAE

Odontaster hispidus Verrill.

Family GONIASTERIDAE

Pseudarchaster concinnus Verrill.
Pseudarchaster parelii (Düben and Koren).
Pseudarchaster ordinatus Verrill.
Paragonaster grandis H. L. Clark.
Mediaster pedicellaris (Perrier).
Tessellaster notabilis H. L. Clark.
Ceramaster grenadensis (Perrier).
Nymphaster ternalis (Perrier).
Nymphaster arenatus (Perrier).
Nymphaster subspinosus (Perrier).
Blakiaster conicus Perrier.
Rosaster alexandri (Perrier).
Peltaster hebes Verrill.
Goniaster cuspidatus Gray.
Plinthaster dentatus (Perrier).
Plinthaster productus A. H. Clark.
Litonaster intermedius (Perrier).
Astroceramis brachyactis H. L. Clark.

[4] *Asterias vestita* Say, Jour. Acad. Nat. Sci. Philadelphia, vol. 5, p. 143 1825.

[5] *Asterias clathrata* Say, 1825, is preoccupied by *Asterias clathrata* Pennant, 1777, but nothing would be gained by displacing this well established name.

Lydiaster americanus A. H. Clark.
Circeaster occidentalis H. L. Clark.
Anthenoides peircei Perrier.

Family OREASTERIDAE

Oreaster reticulatus (Linné).

Family LINCKIIDAE

Linckia bouvieri Perrier.
Linckia guildingii Gray.
Linckia nodosa Perrier.
Copidaster lymani A. H. Clark.
Hacelia floridae (Perrier).[6]
Ophidiaster guildingii Gray.
Ophidiaster bayeri A. H. Clark.

Family GANERIIDAE

Leilaster radians (Perrier).[7]

Family PORANIIDAE

Marginaster pectinatus Perrier.

Family ASTERINIDAE

Asterina folium Lütken.
Stegnaster wesseli (Perrier).

Family ECHINASTERIDAE

Thyraster serpentarius (Müller and Troschel).
Echinaster modestus Perrier.
Echinaster sentus (Say).
Henricia antillarum (Perrier).
Henricia microspina Verrill.
Henricia sexradiata (Perrier).

Family SOLASTERIDAE

Solaster caribbeus Verrill.
Lophaster furcifer (Düben and Koren).
Lactmaster spectabilis (Perrier).

Family PTERASTERIDAE

Pteraster caribbaeus Perrier.
Pteraster militarioides H. L. Clark.
Pteraster rugosus H. L. Clark.
Pteraster stoibe H. L. Clark.
Hymenaster regalis Verrill.

Family BRISINGIDAE

Odinia pandina Sladen.
Freyella mexicana A. H. Clark.

Family ZOROASTERIDAE

Zoroaster ackleyi Perrier.
Mammaster sigsbei (Perrier).

[6] Includes *Ophidiaster floridae* Perrier, 1881; *O. alexandri* Verrill, 1915; *O. pinguis* H. L. Clark, 1941; and *Hacelia superba* H. L. Clark, 1921.

[7] Given by Perrier as *Korethraster radiaas*, *Lophaster radians*, *Solaster radians*, and *Korethraster hispidus*.

Family ASTERIIDAE

Pedicellaster pourtalèsi Perrier.
Coronaster briareus (Verrill).
Asterias crassispina H. L. Clark.
Asterias forbesi (Desor).
Stephanasterias gracilis (Perrier).
Eustolasterias angulosa (Perrier).
Eustolasterias contorta (Perrier).

OPHIUROIDEA

Family OPHIOMYXIDAE

Ophiomyxa brevicauda Verrill.
Ophiomyxa flaccida (Say).
Ophiomyxa tumida Lyman.
Ophiobyrsa serpens Lyman.
Ophiobrachion uncinatus Lyman.
Ophiogeron granulatus (Lyman).
Ophiophrixus quadrispinosus (Koehler).
Ophiosciasma granulatum Lyman.
Ophioscolex disacanthus H. L. Clark.
Ophioscolex stimpsonii Lyman.
Ophioscolex tropicus Lyman.
Ophioleptoplax atlanticus Koehler.

Family TRICHASTERIDAE

Asteroschema arenosum Lyman.
Asteroschema brachiatum Lyman.
Asteroschema elongatum Koehler.
Asteroschema intectum Lyman.
Asteroschema laeve (Lyman).
Asteroschema nuttingii Verrill.
Asteroschema oligactes (Pallas).
Asteroschema tenue Lyman.
Ophiocreas lumbricus Lyman.
Ophiocreas spinulosus Lyman.
Asteronyx loveni Müller and Troschel.
Astrodia tenuispina (Verrill).

Family GORGONOCEPHALIDAE

Astrogomphus rudis Verrill.
Astrogomphus vallatus Lyman.
Asteroporpa annulata Lütken.
Asteroporpa lindneri A. H. Clark.
Asteroporpa pulchra H. L. Clark.
Schizostella bifurcata A. H. Clark.
Astrocnida isidis Lyman.
Astrospartus mucronatus (Lyman).
Astrophytum muricatum (Lamarck).
Astrocyclus caecilia (Lütken).
Astrocaneum herrerai (A. H. Clark).

Family HEMIEURYALIDAE

Ophiochondrus convolutus Lyman.
Ophiochondrus crassispinus Lyman.
Ophiochondrus gracilis Verrill.
Ophiochondrella squamosa (Lyman).
Sigsbeia conifera Koehler.
Sigsbeia murrhina Lyman.
Ophioplus tuberculosus (Lyman).

Family OPHIACANTHIDAE

Ophiolebes humilis (Lyman).
Ophiacantha affinis Koehler.
Ophiacantha aspera Lyman.
Ophiacantha curima H. L. Clark.
Ophiacantha echinulata Lyman.
Ophiacantha ensifer (Verrill).
Ophiacantha hirsuta Lyman.
Ophiacantha mesembria H. L. Clark.
Ophiacantha pentacrinus Lütken.
Ophiacantha robusta (Koehler).
Ophiacantha scutata Lyman.
Ophiacantha stellata Lyman.
Ophiacantha valenciennesi Lyman.
Ophiothamnus exiguus (Lyman).
Ophiothamnus minimus (Koehler).
Ophiothamnus vicarius Lyman.
Ophiomitrella laevipellis (Lyman).
Ophiomitra ornata Verrill.
Ophiomitra valida Lyman.
Ophioplinthaca dipsacos (Lyman).
Ophioplinthaca incisa (Lyman).
Ophiocamax austera Verrill.
Ophiocamax fasciculata Lyman.
Ophiocamax hystrix Lyman.
Ophioprium cervicorne (Lyman).
Ophiacanthella troscheli (Lyman).
Ophiotreta affinis Koehler.
Ophiotreta lineolata (Lyman).
Ophiotreta littoralis (Koehler).
Ophiotreta mixta (Lyman).
Ophiotreta sertata (Lyman).
Ophialcaea nuttingii Verrill.
Ophioconis miliaria Lyman.

FAMILY OPHIOMYCETIDAE

Ophiomyces frutectosus Lyman.
Ophiomyces mirabilis Lyman.

Family AMPHIURIDAE

Amphiura diducta Koehler.
Amphiura duplicata Koehler.
Amphiura fibulata Koehler.
Amphiura grandisquama Lyman.
Amphiura kinbergiensis Koehler.
Amphiura kükenthali Koehler.
Amphiura lunaris Lyman.
Amphiura otteri Ljungman.
Amphiura palmeri Lyman.
Amphiura semiermis Lyman.
Amphiura stimpsonii Lütken.
Hemipholis elongata (Say).
Ophiophragmus wurdemannii (Lyman).
Ophiophragmus brachyactis H. L. Clark.
Amphipholis abnormis (Lyman).
Amphipholis gracillima (Stimpson).
Amphipholis squamata (Delle Chiaje).
Ophiostigma isacanthum (Say).
Amphiodia pulchella (Lyman).
Amphiodia repens (Lyman).
Ophiocnida cubana A. H. Clark.
Ophiocnida filogranca Lyman.
Ophiocnida scabriuscula (Lütken).
Amphioplus abditus (Verrill).
Amphioplus cuneatus (Lyman).
Amphioplus tumidus (Lyman).
Amphilimna olivacea (Lyman).
Amphitarsus mirabilis H. L. Clark.

Family OPHIACTIDAE

Ophiactis dispar Verrill.
Ophiactis duplicata (Lyman).
Ophiactis loricata Lyman.
Ophiactis mülleri Lütken.
Ophiactis plana Lyman.
Ophiactis savignyi (Müller and Troschel).

Family OPHIOTRICHIDAE

Ophiothrix angulata (Say).
Ophiothrix brachyactis H. L. Clark.
Ophiothrix lineata Lyman.
Ophiothrix örstedii Lütken.
Ophiothrix suensonii Lütken.

Family OPHIOCHITONIDAE

Ophiochiton grandis Verrill.
Ophioplax ljungmani Lyman.
Ophioplax pardalis H. L. Clark.
Ophioplax reducta (Koehler).
Ophioplax spinulifera H L. Clark.
Ophionereis reticulata (Say).

Family OPHIOCOMIDAE

Ophiocoma echinata (Lamarck).
Ophiocoma pumila Lütken.
Ophiocoma riisei Lütken.
Ophiopsila fulva Lyman.
Ophiopsila hartmeyeri Koehler.
Ophiopsila maculata (Verrill).
Ophiopsila riisei Lütken.

Family OPHIODERMATIDAE

Ophioderma appressum (Say).
Ophioderma brevicaudum Lütken.
Ophioderma brevispinum (Say).
Ophioderma cinereum Müller and Troschel.
Ophioderma pallidum (Verrill).
Ophioderma rubicundum Lütken.
Ophiarachnella angulata (Lyman).
Ophiarachnella petersi (Lyman).
Bathypectinura lacertosa (Lyman).

Family OPHIOLEPIDAE

Ophiomastus secundus Lyman.
Amphiophiura metabula H. L. Clark.
Amphiophiura oedignatha H. L. Clark.
Amphiophiura sculptilis (Lyman).
Ophiura acervata (Lyman).
Ophiura falcifera (Lyman).
Ophiura irrorata (Lyman).
Ophiura lepida (Lyman).
Ophiura ljungmani (Lyman).

Ophiomusium acuferum Lyman.
Ophiomusium armigerum Lyman.
Ophiomusium dyscritum (H. L. Clark.)
Ophiomusium eburneum Lyman.
Ophiomusium eburneum var. *eburneum* Lyman.
Ophiomusium eburneum var. *elegans* Verrill.
Ophiomusium leptobrachium H. L. Clark.
Ophiomusium lymani Wyville Thomson.
Ophiomusium microporum H. L. Clark.
Ophiomusium moniliforme H. L. Clark.
Ophiomusium monoplax H. L. Clark.
Ophiomusium oligoplacum H. L. Clark.
Ophiomusium planum Lyman.
Ophiomusium rugosum Koehler.
Ophiomusium sculptum Verrill.
Ophiomusium serratum Lyman.
Ophiomusium stellatum Verrill.
Ophiomusium testudo Lyman.
Ophiomusium validum Ljungman.
Ophiolipus agassizii Lyman.
Ophiothyreus goësii Ljungman.
Ophioceramis rugosa H. L. Clark.
Ophiozona impressa (Lütken).
Ophiozonella clypeata (Lyman).
Ophiozonella granulifera H. L. Clark.
Ophiozonella marmorea Lyman.
Ophiozonella nivea (Lyman).
Ophiozonella nivea var. *compta* (Verrill).
Ophiozonella nivea var. *nivea* (Lyman).
Ophiozonella tessellata (Lyman).
Ophiomidas dubius (Lyman).
Ophiolepis elegans Lütken.
Ophiolepis paucispina (Say).

Family OPHIOLEUCIDAE

Ophiopaepale goësiana Ljungman.
Ophiopyren longispinus Lyman.
Ophiernus adspersus Lyman.

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THE HOLOTHURIANS OF THE GULF OF MEXICO

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The holothurians constitute one of the smaller groups of Recent echinoderms. They occur widespread in the sea, ranging from the shores of the Arctic to the greatest depths of the ocean and particularly abundant in the tropical shallow waters, especially in the coral reef zone. They are predominately bottom forms, though a few are adapted for an exclusive pelagic mode of life, and some have been observed actively swimming.

Except for the larger members of the order they are less likely to be noticed than other echinoderms. For one thing they have thoroughly masked their original five-rayed structure by developing a secondary bilaterality, with a strong muscular system and reduction—in most forms—of the calcareous skeleton; hence they can contract into shapeless lumps or seek shelter in narrow crevices or burrow in sand or mud. In addition, many species dissolve into slime when taken out of water, so it is certain that many specimens never reach the museum collections, even if a careful collector has succeeded in capturing them. It is sometimes difficult to give good description of these forms as their bodies so often are contorted when preserved; also, the number of tube feet frequently increases with age, and the spicules in the skin are apt to undergo profound changes during the animal's life. One finds, therefore, the older literature cluttered with worthless species, based on poorly preserved specimens or immature or aged individuals.

The West Indian region is considered one of the best explored in the world, but our knowledge of the distribution of the holothurians there is still incomplete, and this is particularly true of the northern section—the Gulf of Mexico. In some respects this is an advantage as the worker can begin with a clean slate, free from old records of species which impossibly could have been collected there.

During the last 20 years there has been an increasing interest in the biology of the Gulf area, and material of holothurians has steadily been coming in to the Museum of Comparative Zoology, Harvard College, for identification. It may be worth noting that the only new shallow water dendrochirote added to the West Indian fauna since 1930 came from Louisiana; also, that the *Atlantis* expeditions around Cuba have added a number of new species (or species new to the region), and some of these extend their range into the Gulf area along the north coast of Cuba.

Biologically, one can roughly divide the area under consideration into two zones: the shallow water zone, from shore down to about 200 fathoms—about as deep as one possibly can dredge with a small boat—and the deep water zone which demands a specially equipped vessel with complicated collecting apparatus. The shallow water zone can again be divided into the southern part with coral reefs, that is, the southern part of Florida, the north coast of Cuba, and Yucatán—with a comparatively rich and diversified holothurian fauna—and the barren sandy or muddy stretches along the eastern shores of Mexico, the Gulf States, and most of the western coast of Florida. This region is characterized by an impoverished fauna of burrowing forms which in suitable sheltered localities may occur in large numbers. For the whole shallow water area one can predict that the fauna may change locally from year to year as it undoubtedly does in other parts of the West Indies. The hurricanes may play havoc with large areas both in the southern coral reef region and along the endless stretches of mud flats and sand bars which festoon the northern part of the Gulf, and it may take several years before larvae from individuals living at greater and more secure depths have been able to settle down and re-populate a denuded area again.

The deep water zone will probably prove to consist of two areas, the vast muddy expanses, mostly inhabited by Elasipoda which are adapted

to slide over the slimy bottom, or burrowing forms as the Molpadonia and deep water Apoda, and the ledges along the north coast of Cuba and Yucatán with a depth of 200 to 500 fathoms and inhabited by offshots of the shallow water fauna, mostly Aspidochirota and Synallactidae.

In 1930 an attempt was made to trace the origin of the West Indian holothurian fauna on the basis of what was then known. The following 20 years have added so much to our knowledge about the distribution of the holothurians of the American waters, the result of the Hancock expeditions along the west coast of Mexico and Central America and the Harvard–Havana expeditions around Cuba, that many of the statements set down then have had to be modified or entirely reversed.

The deep water forms, the Elasipodae, Synallactidae, and a few Holothuriidae, represent a selection of the Atlantic fauna. Most of them are typical mud dwellers which occur widespread in the Atlantic Ocean in deep water, but the *Atlantis* expeditions have added a number of forms hitherto known only from the eastern part of the Atlantic occurring close to the shore and from moderate depth, 200 to 500 fathoms or so. Some of these have been taken inside of the Gulf area along the northern coast of Cuba, and they may very likely prove to be a characteristic element in the southern part of the Gulf.

The order Molpadonia have a few representatives from moderate to great depth. With a single exception, the widespread *Molpadia musculus*, they all appear to be endemic, though one may expect that most of them have a parallel form in the Pacific. The single representative of the order Apoda is known from deeper water off the Atlantic Coast of North America, and in the end it may be united with a closely related species reported from the eastern Pacific.

Among the typical shallow water forms, which mostly are taken at low tide or a few fathoms depth though some go down to almost 200 fathoms, we find that the Aspidochirota have no affinities with the eastern Atlantic (*Holothuria impatiens* is a circumtropical form, while *H. mexicana* and *Stichopus badionotus*, though reported from the eastern Atlantic, appear not to belong there; it may be either wrong labeling, or they may have become accidentally introduced without being permanently established). The Aspidochirotes have their closest affinities with the Indo-Pacific fauna; a few somewhat similar species occur also in the Panamic region, but we are not able to speak of truly parallel forms. On the other hand, the dendrochirotes which 20 years ago were considered endemic have now, thanks to the Hancock expeditions, been found to have in most cases a parallel form in the Panamic region but no close affinities with the remaining part of the Pacific Ocean nor with the eastern Atlantic. An exception is *Thyone inermis*, a Mediterranean form of which immature specimens have been taken, off and on, around Florida and at Tobago but not in the Gulf itself. Some dendrochirotes appear to be absent in the West Indies as a whole but occur in the northern part of the Gulf and along the Atlantic seaboard (*Thyone briareus* and *Thyonella gemmata*). There is only one true shallow water form of the order Molpadonia, though others have been taken in abnormally shallow water; this species, *Paracaudina obesacauda*, is, as far as known, restricted to the Gulf, and the genus is not otherwise known from the Atlantic Ocean. A number of closely related species in shallow water are found in the Pacific, ranging from Chile northward to Alaska, from Japan, China, Australia to New Zealand. When it comes to the order Apoda, our knowledge is still most unsatisfactory. The few, purely tropical species known from the West Indies will undoubtedly be found widespread in the southern part of the Gulf, on the reefs, while offshots from the forms found along the Atlantic seaboard may be expected in muddy and sandy localities between Florida and Texas and possibly farther south along the east coast of Mexico. Nothing can be said about the affinities with the Panamic fauna of Apoda as it is still almost unknown. Very likely it is almost nonexisting as much of the shoreline of the west coast of Mexico and Central America is ill-suited for these forms. With the fauna of Apoda from the eastern Atlantic and the Mediterranean there seem to be no close affinities.

TECHNIQUE

Holothurians may be anesthetized with chloretone or Epsom salt, or even stale sea water. By slowly adding alcohol one is often able to have them preserved in reasonably well-expanded condition. Large species may later have an incision made in the skin so that alcohol can penetrate

into the body cavity. As it often is impossible to bring back the large individuals one can make a note of their length and width, color, arrangement of tube feet, papillae, or other features, and preserve some pieces of the skin with a tag tied to it; one should take a skin sample from the dorsal side as well as from the ventrum as the spicules often are quite different in these two regions. Formalin must never be used as it dissolves the spicules and makes the tissue soft.

The gross anatomical features can be found listed in almost any zoological textbook. For examination of the spicules one places a small piece of skin on a slide, noting whether it is from dorsal or ventral side, or elsewhere, and after most of the alcohol has evaporated one adds a few drops of fresh chlorox or zonite or a similar chlorine bleaching compound. It pays to follow the disintegration of the tissue to estimate the position of the different types of spicules. Often one can get the outer spicules off by placing the skin with the outer side downward in the liquid for a short time. This is of special advantage when the external spicules are small or so few that they easily disappear among those of the deeper layer. Special preparations may often be made of the tube feet to ascertain whether an end plate or a trace of such is present, and how the walls are armed; many times juvenile spicules are retained near the tip of papillae. In the dendrochirota the introvert, the retractile thin-skinned part behind the tentacles, contains usually characteristic spicules, as do also the tentacles. The size of the animal must be noted since there often is considerable difference in the size and shape of the spicules in the young and the aged individuals. In some forms the spicules are reduced with age and may become completely resorbed; in others, they grow heavier and more complex.

Extremely small individuals,a few millimeters long, are often difficult to identify. Sometimes they have still only simple perforated plates, and when the first typical spicules appear they are in many forms scaled down to the animal's size. In some forms there is a period during which the spicules are excessively large, and these spicules may be found preserved near the tip of the papillae when they have disappeared in other places.

Permanent slides can be made by rinsing off the chlorine solution with distilled water and letting the slide go through alcohol-xylol-balsam. Great care must be exercised not to have the slides contaminated with spicules from earlier preparations. With important specimens it is wise to use a new eye dropper and a fresh bottle of chlorine solution.

KEY TO THE ORDERS

1. Animals with disk-shaped tentacles 2
1. Animals not with disk-shaped tentacles 3
2. No respiratory trees present. Exclusively deep water forms ..... 1. Elasipoda, p. 383
2. Respiratory trees present. Shallow water to deep water forms ..... 2. Aspidochirota, p. 384
3. Tentacles dendritic, 10 to 20 in number; numerous tube feet. Plankton feeders. Clings to the substratum or buried in mud or sand, except for the tentacles and the anal end ..... 3. Dendrochirota, p. 394
3. Tentacles not dendritic, feather-shaped or with few lateral digits 4
4. Tentacles 15, small, in a terminal circle, with few digits. Tube feet reduced to anal papillae. Body barrel-shaped with a shorter or longer "tail." Burrows in mud ..... 4. Molpadonia, p. 405
4. Tentacles 10 (or 12–13) with few to many digits, sometimes feather-shaped. Tube feet totally lacking. Body worm-like often able to contract transversely so the hind end drops off (may later be regenerated). Among coral fragments or burrowing in sand or mud ..... 5. Apoda, p. 406

Order 1 ELASIPODA

In the Gulf of Mexico only three representatives have so far been taken of this remarkable order which first became known when the *Challenger* explored the deepest parts of the oceans in the 1870's. On the whole, one can say that the deeper parts of the Gulf of Mexico represent a true "Mediterranean" type of water body, with few species, but nevertheless one may expect almost any species known from the Atlantic Ocean. In case other species than those listed below should be found, it will be necessary to consult more extensive reports, such as Mortensen's, The Echinoderms of the British Isles, 1927, or Deichmann's 1930 and 1940 papers.

Family PSYCHROPOTIDAE

KEY TO THE GENERA AND SPECIES TAKEN IN THE GULF OF MEXICO

1. Dorsal side with a "hump"-like appendage on the posterior part. Spicules dorsal crosses, with strongly curved arms and a central spine surrounded by four smaller ones. Color deep purplish. Genus 1. *Euphronides*.
Euphronides violacea Perrier, p. 384
1. Dorsal side without a posterior "hump." Genus 2. *Benthodytes* 2
2. Flattened form, short, with a broad lateral swimming brim of papillae. Spicules simple spinous rods. Deep purple.
1. *Benthodytes typica* Théel, p. 384
2. More or less vaulted form, elongate, with narrow brim of papillae. Spicules large crosses with curved arms and one to three stout, spinous projections arising from the center. Color reddish to deep purple.
2. *Benthodytes lingua* Perrier, p. 384

Genus 1 EUPHRONIDES Théel, 1881

1 *Euphronides violacea* Perrier

Euphronides violacea Perrier, 1896, p. 102; 1902, p. 438, pl. 20, fig. 14; Deichmann, 1930, p. 128.

Diagnosis.—Flattened body with mouth and anus ventral, 10 to 20 tentacles, narrow lateral brim of small papillae. Dorsally four to six pairs of papillae placed anteriorly and an unpaired hump arising some distance from the posterior margin. Spicules, dorsally large, curved crosses with one large conical spine surrounded by four smaller ones; ventrally scattered delicate crosses, almost flat. Type: Paris. Type locality: Coast of Morocco. Distribution: Eastern Atlantic; in the western part from the Lesser Antilles and Gulf of Mexico, from 655 to 2,120 fathoms.

Genus 2 BENTHODYTES Théel, 1881

1 *Benthodytes typica* Théel

Benthodytes typica Théel, 1882, p. 103; 1886a, p. 2; Deichmann, 1930, p. 123.

Diagnosis.—Flat, short form (15 cm.) with wide swimming-brim of closely placed papillae. Double row of small pedicels in midventral ambulacrum. Deep purple in color. Spicules scattered, spinous rods. Type: British Museum. Type locality: Off Gibraltar. Distribution: Eastern Atlantic; in the West Indies, common in the Gulf of Mexico, along the Lesser Antilles and also known from off the coast of New England, from 172 to 766 fathoms.

It is seldom that one gets more than a bunch of broad muscle bands and some shreds of skin. Nevertheless, it is usually possible to recognize the animal on account of the short body length and the simple spicules. It lives on soft mud bottom

2 *Benthodytes lingua* Perrier

Benthodytes lingua Perrier, 1896, p. 902; 1902, p. 466, pl. 12, figs. 1–2; pl. 21, figs. 1–9; Deichmann, 1930, p. 124; 1940, p. 200, pl. 35, figs. 3–4.

Diagnosis.—Large form, 30 cm., with 15 ventral tentacles, a narrow brim of small papillae and a double row of feet in the midventral radius. Dorsally, a few, insignificant papillae. Color pale reddish to deep purplish. Enormous crosses with curved spinous arms and one to three stout spinous projections from the center of the cross. Type: Paris. Type locality: Off Morocco. Distribution: Eastern Atlantic; in the western part known from the Gulf of Mexico and also off the coast of New England from 470 to 1,200 fathoms.

Order 2 ASPIDOCHIROTA Grube

KEY TO THE FAMILIES

1. No free tentacle ampullae. Deep water forms ..... 1. Synallactidae, p. 384
1. Free tentacle ampullae. Mostly shallow water forms 2
2. Genital organs in two tufts. Large, thick-skinned forms ..... 2. Stichopodidae, p. 387
2. Genital organs in one tuft on left side of dorsal mesentery. Large to small forms ..... 3. Holothuriidae, p. 388

Family 1 SYNALLACTIDAE

KEY TO THE GENERA REPRESENTED IN THE GULF OF MEXICO

1. Spicules almost lacking. Anus often in a vertical furrow. Skin thick, gelatinous, often covered by sand or minute shells ..... 1. *Pseudostichopus* Théel, p. 395
1. Spicules present. Anus not in a vertical furrow 2

2. Spicules large tables with disk developed as a cross; rarely arms of cross united so a complete disk is formed. Large, thick-skinned forms with ventral side set off as a sole with marginal papillae ..... 4. *Bathyplotes* Oestergren, p. 386
2. Spicules small to large tables; disk not cross-shaped 3
3. Appendages large papillae and feet, all in distinct rows. Tables of varying size, often the large ones with spire reduced. 5. *Amphigymnas* Walsh, p. 387
3. Appendages small, scattered or marginal 4
4. Numerous tube feet, resembling short threads, distributed over most of the sack-like body .. 2. *Mesothuria* Ludwig, p. 385
4. Few marginal feet, wart-like ..... 3. *Zygothuria* Perrier, p. 386

Genus 1 PSEUDOSTICHOPUS Théel, 1882

Of the seven incompletely known species reported from the Atlantic Ocean, one is listed from the Gulf of Mexico. For the others which very likely may belong to the fauna, see Mortensen, 1927, p. 367, or Deichmann, 1930, p. 86.

Pseudostichopus occultatus v. Marenzeller

Pseudostichopus occultatus v. Marenzeller, 1893a, p. 15, pl. 4, fig. 9; Deichmann, 1930, p. 89; 1940, p. 190.

Diagnosis.—Small species, 4 to 6 cm., body normally covered with *Creseis*-shells, etc. Larger tube feet along sides of body. A few perforated plates usually found near anus; tentacles with curved rods; gonads with delicate crosses. Type: Possibly in Vienna. Type locality: Eastern Mediterranean. Distribution: Eastern Atlantic; northwest of Cuba. From 160 to 1,100 fathoms. The covering of Pteropod shells seems to be characteristic of this small species.

Genus 2 MESOTHURIA Ludwig, 1894

KEY TO THE SPECIES REPORTED FROM THE GULF OF MEXICO

1. Deposits triradiate tables ..... 1. *Mesothuria maroccana* Perrier, p. 385
1. Deposits quadriradiate tables 2
2. Feet of almost uniform size scattered over most of the upper and lower side ..... 2. *Mesothuria verrilli* Théel, p. 385
2. Feet dorsally small, absent on most of the ventrum 3
3. Tables of moderate size with one circle of about eight holes, sometime a few accessory ones 3. *Mesothuria intestinalis* (Ascanius and Rathke), p. 385
3. Tables with enormous disks with numerous holes in several circles ..... 4. *Mesothuria gargantua* Deichmann, p. 386

1 *Mesothuria maroccana* Perrier

Mesothuria maroccana Perrier, 1902, p. 312, pl. 16, figs. 32–35; Deichmann, 1930, p. 97, pl. 7, figs. 2–7; 1940, p. 191.

Diagonsis.—Small form, 4 to 8 cm. long, with feet largest along the flanks, well-developed on the dorsum and totally lacking on the ventrum. Spicules, regular tables mostly with six holes; margin smooth or undulating; spire composed of three rods and ending in three diverging arms with few teeth. Type: Paris. Type locality: Off Morocco, 2,105 meters. Distribution: Eastern Atlantic; also widespread in the West Indies; in the Gulf of Mexico reported from San Nicholas Channel, northern Cuba, 500 fathoms. From 500 to 1,350 fathoms.

2 *Mesothuria verrilli* (Théel)

Holothuria verrilli (partim) Théel, 1886b, p. 6.
Mesothuria verrilli Deichmann, 1930, p. 93, pl. 6, figs. 1–8; 1940, p. 192.

Diagnosis.—Up to 30 cm. long. Feet small, thread-like, more or less uniformly scattered, absent on anterior part of ventrum. Spicules tables with regular to irregular disk with about eight holes, sometimes reduced with age. Feet with small tables, often with disk completely resorbed. Type: Museum of Comparative Zoology. Type locality: Ambergris Key, British Honduras. Distribution: Eastern and western Atlantic, from 382 to 1,000 fathoms; in the West Indies common along the Lesser Antilles and recently secured by the *Atlantis* along the north coast of Cuba. The species may be expected off the shores of Yucatán.

3 *Mesothuria intestinalis* (Ascanius and Rathke)

Holothuria intestinalis Ascanius and Rathke, 1805, Fasc. 5, p. 5, pl. 45.
Mesothuria intestinalis Deichmann, 1930, p. 94, pl. 6, figs. 9–10.

Diagnosis.—Elongate thin-skinned form with almost naked ventrum, large lateral feet and smaller dorsal ones. Spicules tables with eight oval holes; feet with end plate and tables of same size and shape as those in the skin. Type: Not

existing. Type locality: Coast of Norway. Distribution: From Murman coast, Norway to the Azores; also in the Mediterranean; in the western Atlantic taken off the Lesser Antilles and off Florida (*Fish Hawk*), 200 fathoms. According to Mortensen (1927), from 10 to 1,000 fathoms. The extreme low depth may refer to the most northern localities; usually the species lives at 200 fathoms or more. As far as the present records go the species is not common in the American waters, but it may very likely occur in numbers on the extensive areas of muddy bottom in the Gulf of Mexico.

4 *Mesothuria gargantua* Deichmann

Holothuria verrilli Théel (partim), 1886b, p. 6.
Mesothuria gargantua Deichmann, 1930, p. 95, pl. 7, fig. 1; 1940, p. 191.

Diagnosis.—Large robust form, 20 cm. long, with stout, cylindrical feet over entire surface except the anterior part of the ventrum; dorsal feet slightly smaller. Spicules tables with irregular disk with numerous holes and four-pillared spire with numerous spines on the top. Feet with vestige of end plate or none; tables as those in the skin. Type: Museum of Comparative Zoology. Type locality: Off Barbados, 394 fathoms. Distribution: Off the Lesser Antilles (*Blake*); north of Cuba (*Atlantis*). From 394 to 500 fathoms. This robust species may possibly be common in deeper water of coasts of Cuba and Yucatán.

Genus 3 ZYGOTHURIA Perrier, 1898

Zygothuria lactea (Théel)

Holothuria lactea Théel, 1886, p. 183.
Zygothuria lactea Deichmann, 1930, p. 108, pl. 8, figs. 8–9; 1940, p. 190.

Diagnosis.—Large flattened forms, 15 cm. long, with few tube feet along the margin. Spicules, fragile tables with six large holes in the disk, and slender, three-pillared spire with either three long, diverging spines or a single pointed rod. Type: British Museum. Type locality: Off New Zealand. Distribution: Widespread in the Pacific and Atlantic Oceans; common along the coast of New England, in the West Indies and also taken in the Gulf of Mexico. From about 350 to 1,000 fathoms.

The *Albatross* collected it in various localities in the Gulf, while the *Atlantis* dredged it in San Nicholas Channel, northern Cuba. One would expect it to be one of the most common species in the muddy part of the Gulf.

Genus 4 BATHYPLOTES Oestergren, 1896

KEY TO THE SPECIES FOUND IN THE GULF OF MEXICO

1. Disk of tables often forming a complete circle with a large number of large holes in each of the four sections. Dorsal side flattened; ventral side with small fungiform papillae in two bands ... 3. *Bathyplotes bigelowi* Deichmann, p. 387
1. Disk of tables cross-formed ... 2
2. Arms with few holes, often incomplete; spire smooth, without teeth. Dorsal side high, vaulted with large papillae; ventral side with large fungiform papillae ... 2. *Bathyplotes pourtalesi* (Théel), p. 386
2. Arms with numerous small holes; spire with teeth along the sides. Dorsal side flattened; no large fungiform papillae on the ventrum (if any are present they are quite small) ... 1. *Bathyplotes natans* (M. Sars), p. 386

1 *Bathyplotes natans* (M. Sars)

Holothuria natans M. Sars, 1868, p. 4.
Bathyplotes natans Deichmann, 1930, p. 100, pl. 9, figs. 1–2, 8.

Diagnosis.—Flattened, large form with marginal row of papillae; dorsal side with few papillae in indistinct rows. Ventral side with lateral rows of appendages and sometimes some scattered on the ventral sole but none in the midventral ambulacrum. Spicules tables with cross-shaped disk with a large number of small holes. Type: Not existing. Type locality: Lofoten, Norway. Distribution: In the eastern Atlantic from Lofoten to Cape Verdes, from 100 to 800 fathoms; in the West Indies reported from the Gulf of Mexico, 335 and 337 fathoms depth (*Albatross* station 2396 and 2398). The species is also reported from the Japanese waters (Mortensen, 1927, p. 385), but the latter record needs reinvestigation.

2 *Bathyplotes pourtalesi* (Théel)

Stichopus pourtalesi Théel, 1886a, p. 4.
Bathyplotes pourtalesi, Deichmann, 1930, p. 102, pl. 9, figs. 3–7; 1940, p. 186, pl. 31, figs. 3–4.

Diagnosis.—Large form, 20 cm. or more, with high, vaulted dorsal side, thick-skinned with large papillae (often thrown off in long strips); ventral side with large fungiform papillae. Spicules

tables with smooth four-pillared spire and few holes in the tip of the arms of the disk. Type: Museum of Comparative Zoology. Type locality: Off St. Kitts. Distribution: Known from off the Canaries, in the eastern part of the Atlantic, off the Lesser Antilles, Ambergris Key, British Honduras, and the northeast coast of Cuba. About 200 to 600 fathoms.

Although it has not been reported in the Gulf itself, it is most likely that the gap between northeast Cuba and Ambergris Key will be closed when more extensive dredging is undertaken in the Gulf. It is seldom that one gets a complete specimen, but the large fungiform papillae and the spicules should make it easy to recognize this species.

3 *Bathyplotes bigelowi* Deichmann

Bathyplotes bigelowi Deichmann, 1940, p. 187, pl. 31, figs. 1–2.

Diagnosis.—Large form, 25 cm. Resembles *B. natans* but has two bands of large fungiform papillae on the ventral side, and the spicules are large delicate tables usually with a circular disk with large holes in the ends of the four arms. Type: Museum of Comparative Zoology. Type locality: Bahia de Cochinos, southern Cuba. Distribution: Waters around Cuba. From 220 to 320 fathoms. So far it has been reported only in the Gulf, from the northwest coast of Cuba, but it will undoubtedly prove to belong to the fauna of the waters around Yucatán.

Genus 5 AMPHIGYMNAS Walsh, 1891

Amphigymnas bahamensis Deichmann

Amphigymnas bahamensis Deichmann, 1930, p. 107, pl. 9, fig. 9, pl. 10, figs. 1–6; 1940, p. 189, pl. 32, figs. 1–10.

Diagnosis.—Large species with skin rigid from spicules. Resembles a *Synallactes*, with four rows of conical papillae on the dorsum, a lateral row of stouter conical appendages and a midventral double row of smaller ones. Inner anatomy like that of *Synallactes* but muscle bands undivided.

Spicules large to small tables with mostly four central holes and smaller marginal ones; spire mostly with four pillars, often reduced, besides large perforated plates. Ventral appendages with or without end plate, with walls packed with supporting rods with dentate edge, and small tables with three to four short pillars in spire. Dorsal and lateral papillae with curved supporting rods and tables of varying size but apparently no trace of end plate. Color lavender, quickly reduced to pure white in alcohol. Type: United States National Museum. Type locality: Between Bahamas and Cape Fear, 270 fathoms. *Albatross* station 2666. Distribution: Known from the type locality and the waters around Cuba and Florida. In the Gulf taken south of the Mississippi Delta (*Oregon* station 384, 29°10′ N., 88°00′ W., 265 to 300 fathoms).

The largest specimen measures 33 cm. It was collected in June 1951 by the *Oregon* and showed four months later a beautiful lavender color which probably in a few years will have completely faded into a pure white. The spicules of the few specimens which have been examined show great variation, but there seems no doubt that they all belong to the same species. It has so far never been taken in the eastern Atlantic, but most likely it does occur there. The only other representative of the genus is found in the Indian Ocean (see Deichmann 1930, p. 107).

Family 2 STICHOPODIDAE

KEY TO THE GENERA KNOWN FROM THE GULF OF MEXICO

1. Large, thick-skinned forms with feet in crowded bands on the ventral side and large warts on the vaulted dorsal side. Spicules tables; C-shaped bodies present in some species ..... 1. *Stichopus* Brandt, p. 387
1. Large thick-skinned forms with numerous tube feet scattered all over the body but not forming a ventral sole, nor has the dorsal side distinct warts. Spicules minute grains, and C-shaped bodies ..... 2. *Astichopus* H. L. Clark, p. 388

Stichopus Brandt, 1835

1. Deep water form (200 fathoms). Prominent lateral brim of papillae. Spicules large tables with up to 50 holes in disk ..... 1. *Stichopus regalis* (Cuvier), p. 388
1. Shallow water (reef dweller, probably down to 25 to 30 fathoms depth). No prominent lateral brim of papillae. Spicules small tables with few holes in the disk; often also C-shaped bodies ..... 2. *Stichopus badionotus* Selenka, p. 388

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Genus 1 STICHOPUS Brandt, 1835

1 *Stichopus regalis* (Cuvier)

Holothuria regalis Cuvier, 1817, p. 22.
Stichopus regalis Deichmann, 1940, p. 193, pl. 32, figs. 1–8.

Diagnosis.—Large form, up to 32 cm. long, with lateral row of papillae, ventrum with numerous cylindrical indistinct bands; dorsal side with papillae. Color brownish with white spots on the dorsal side, ventrum paler. Spicules large tables with numerous holes in the disk. Type: Possibly in Paris. Type locality: Mediterranean Sea. Distribution: In the eastern Atlantic from the west coast of Ireland to the Canaries. In the western Atlantic reported for the first time, by the *Atlantis*, west of Havana, at 200 fathoms depth. Lampert (1885, p. 101) reports that it is taken at 2 fathoms depth, but one wonders whether there is not some misunderstanding. Most specimens appear to have come from 50 to 200 fathoms depth, and Nobre (1931, p. 146) mentions that the animal has difficulty in surviving in aquaria.

This represents another of the east Atlantic species which the Harvard-Havana expeditions revealed also existed in the western part. It will probably be found to occur more widespread in the Gulf, at moderate depth, along the northern coast of Cuba and around Yucatán.

2 *Stichopus badionotus* Selenka

FIG. 66: 1–8

Stichopus badionotus Selenka, 1867, p. 316, pl. 18, fig. 26; Deichmann, 1930, p. 80, pl. 5, figs. 30–36; 1940, p. 195.

Diagnosis.—Large, thick-skinned form with cylindrical feet in crowded bands on the ventrum and flanks and dorsum with few large warts. Color varying from deep chocolate brown to almost black or spotted or striped on more yellow ground. Spicules a crowded layer of small tables with few holes in a circle around the low, squat spire; sometimes C-shaped bodies. Type: Museum of Comparative Zoology. Type locality: Florida. Distribution: Seems to be common all over the West Indies including Bermuda, wherever there are suitable localities—quiet pools with eelgrass or sandy patches among coral reefs. It is known from the Florida reefs, the north coast of Cuba, and Yucatán, but it is doubtful whether it is able to live in the northern part of the Gulf.

Crozier (1918) has studied its biology and found that its consumption of sand is not unimportant in the sanitation of the reefs whenever it occurs in large numbers. The animals become easily transformed into slime and are apparently unsuitable for preparation of "trepang" as no animals seem to want to eat them. As in the case of many other marine animals mostly large individuals are known; the young ones must undoubtedly hide in inaccessible spots; they probably grow very fast as Mitsukuri has found in a related species in Japan.

Genus 2 ASTICHOPUS H. L. Clark, 1922

Astichopus multifidus (Sluiter)

Stichopus multifidus Sluiter, 1910, p. 334, text figs. a–b.
Astichopus multifidus Clark, 1922, p. 48; Deichmann, 1930, p. 84, pl. 5, figs. 44–47.

Diagnosis.—Large species, 45 cm. long; body blunt, cylindrical, with tube feet scattered over the entire surface, cylindrical on the ventrum, smaller, more papilliform on the dorsum. Spicules numerous minute grains, collected in heaps, and besides scattered C, S, or O-shaped bodies. The feet have an end plate composed of smaller plates, and the walls contain C-shaped bodies. Type: Hamburg Museum. Type locality: Tortugas. Distribution: Taken at the type locality, also Port Antonio, Jamaica, and the Campeche Bank. Few fathoms depth, down to 8 to 10 fathoms.

While it is easy to recognize this species it is still uncertain whether it belongs in the family Stichopodidae. Although large specimens have been available, the gonads have not been well preserved so it is not certain whether they are in one or two tufts.

Up to recently only few specimens have been observed, but now (1951) H. Hildebrand informed me that the species is "very conspicuous if not abundant in trawl hauls on the Campeche Bank."

Family 3 HOLOTHURIIDAE Ludwig, 1894

KEY TO THE GENERA FOUND IN THE GULF OF MEXICO

1. Anus surrounded by five conspicuous calcified "teeth." Large, clumsy forms with spicules as simple rosettes and short blunt rods; no tables ..... 1. *Actinopyga* Bronn, p. 390
1. Anus not surrounded by five conspicuous calcified teeth. Varying sizes. Spicules of different types. If simple rosettes, no short blunt rods, but tables also present ..... 2. *Holothuria* Linnaeus, p. 390

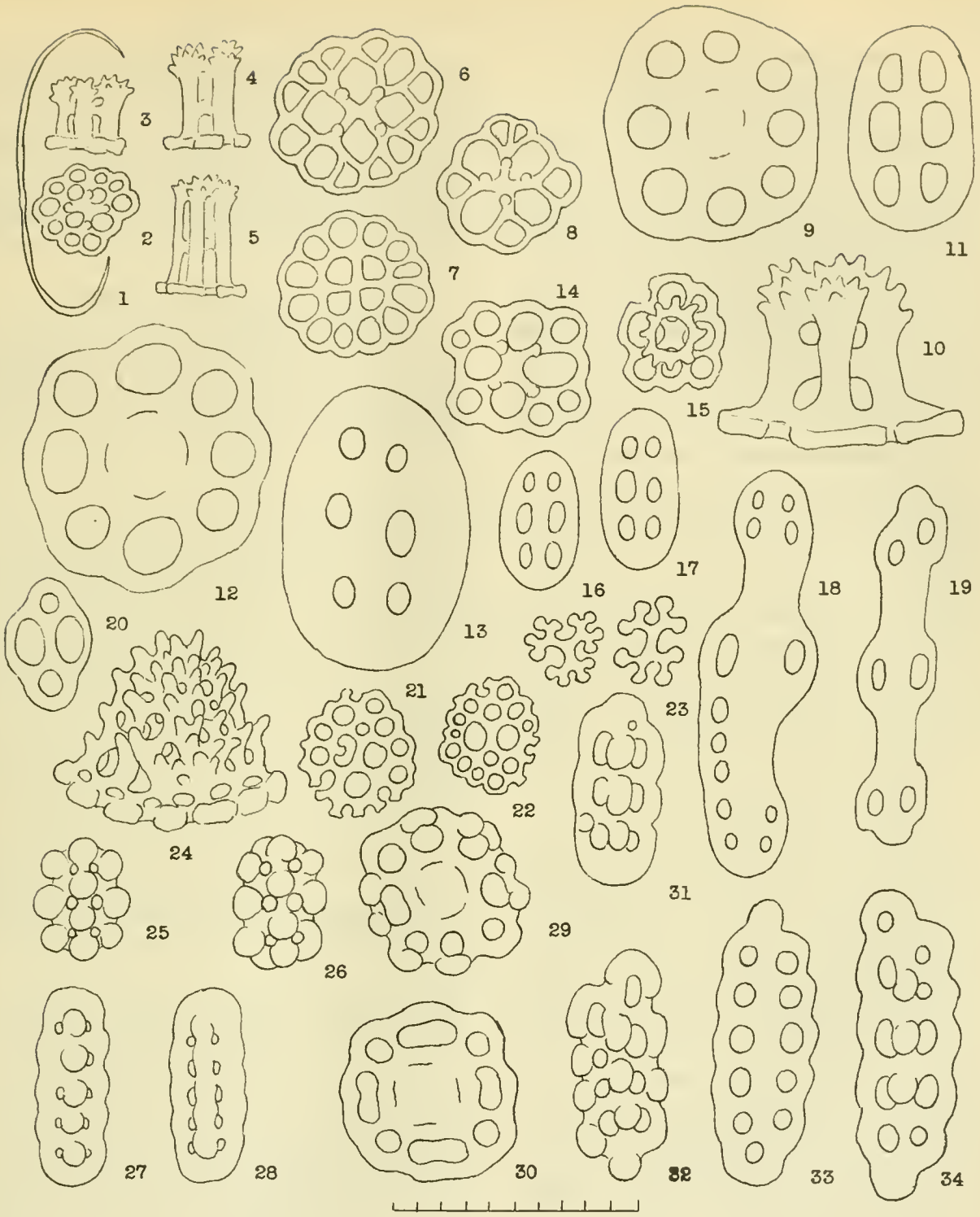

FIGURE 66: 1–34.—*Stichopus badionotus*, p. 388. 1, C-shaped spicules; 2–3, table from body of adult; 4–5, tables from young lateral view; 6–8, disk of tables from young. *Holothuria impatiens* (Forskål), p. 393. 9–10, table, disk and side view; 11, button. *Holothuria parvula* Selenka, p. 392. 12, disk of table; 13, button. *Holothuria arenicola* Semper, p. 393. 14–15, tables; 16–17, buttons; 18–19, long rods or buttons from feet. *Holothuria mexicana* Ludwig, p. 391. 20–22, buttons and plates. *Holothuria floridana* Pourtales, p. 392. 23, typical rosettes. *Holothuria cubana* Ludwig. 24, table, lateral view; 25–28, knobbed buttons, short and long. *Holothuria pseudofossor* Deichmann, p. 394. 29–30, disk of tables; 31–34, knobbed to smooth buttons. Magnification: ×400 Divisions 1/100 mm.

Genus 1 ACTINOPYGA Bronn, 1860

Actinopyga agassizii (Selenka)

Mülleria agassizii Selenka, 1867, p. 311.
Actinopyga agassizii Deichmann, 1930, p. 78, pl. 5, figs. 21–29.

Diagnosis.—Large, stout form, preserved and contracted 20 cm. long, but may very well be almost twice as long when alive. Mouth ventral with 25 to 29 large tentacles; anus with five large anal teeth. Ventral side with numerous cylindrical feet in three bands; dorsal side with small papillae and minute cylindrical feet. Color varying shades of brown, mottled; pedicels and tentacles yellowish. Spicules simple rosettes and short blunt rods. Type: Museum of Comparative Zoology. Type locality: Florida. Distribution: Known from Barbados to Florida; once taken in Bermuda but appear not to be a constant element in that island's fauna (Crozier, 1917d).

As far as known it lives exposed in the sheltered pools of the West Indian reefs. It will most likely turn out to be found also in shallow water around Yucatán.

Genus 2. HOLOTHURIA Linnaeus, 1757

Remarks.—A little more than a dozen species are known from the West Indian region, and although not all have definitely been found inside the Gulf area they are all included in the key.

KEY TO THE SPECIES FOUND IN THE GULF OF MEXICO OR LIKELY TO OCCUR THERE

1. Deep water forms, about 200 fathoms depth 2
1. Shallow water forms, exposed at low tide or down to less than 50 fathoms depth 3
2. Large, soft-skinned form, up to 46 cm. long, color light brown with tips of appendages darker, often a lighter spot around base. Spicules tables and smooth buttons, twisted, incomplete, rarely with one or two knobs on the surface ..... 1. *Holothuria lentiginosa* v. Marenzeller, p. 391
2. Medium-sized forms, up to 15 cm. long; skin stiffened with spicules. Ventrally cylindrical tube feet; dorsally and laterally conical papillae. Spicules small tables with blunt dentate margin and often partly resorbed spire; buttons deformed, knobbed, sometimes with holes obliterated ..... 2. *Holothuria occidentalis* Ludwig, p. 391
3. Dark, blackish or brownish forms, soft-skinned, with numerous cylindrical feet on ventrum. Spicules few, curved rods in the skin. Clings to rocks in the surf zone ..... 3. *Holothuria glaberrima* Selenka, p. 391
3. Not blackish, soft-skinned; not clinging to rocks in the surf zone 4
4. Free-living forms, usually exposed in the tide pools, sometimes with a few bits of seaweeds or sand covering the dorsum 5
4. Normally buried in sand or mud or hiding under rocks or among corallines, etc 7
5. Large, smooth-skinned, form blunt, cylindrical, usually dark above and pinkish below. Spicules small tables and minute perforated plates, mostly with small holes ..... 4. *Holothuria mexicana* Ludwig, p. 391
5. Medium sized forms, not particularly thick-skinned 6
6. Usually brownish in color, sometimes spotted; not strongly warted dorsal side. Spicules tables and simple rosettes. (Young individuals concealed among mangrove.) ..... 5. *Holothuria floridana* Pourtalès, p. 392
6. Colors mixed gray (living animals with specks of yellow red, black, etc.). Dorsal side with distinct rows of low warts. Spicules tables and small plates with two to four large central holes, some small terminal ones and a blunt dentate margin ..... [6. *Holothuria grisea* Selenka, p. 392]
7. Animals normally concealed under rocks or among corallines 8
7. Animals normally buried in sand or mud 10
8. Flattened, yellowish-brownish forms with ventral circle of large tentacles; ventral feet crowded; dorsal side with papillae. Spicules a crowded layer of tables and large oval smooth buttons with comparatively small holes. 7. *Holothuria parvula* Selenka, p. 392
8. Elongate, cylindrical or flask-shaped forms with small terminal tentacles; feet scattered, more papilliform on dorsal side 9
9. Chocolate colored with yellow tentacles. Spicules a crowded layer of tables with tall spire ending in few spines which form a Maltese cross; disk resorbed, except in very small specimens; a few large flat bars beneath the tables, most numerous near the tube feet ..... 8. *Holothuria surinamensis* Ludwig, p. 393
9. Mottled gray, warty, rough to the touch. Spicules a crowded layer of squat tables with squarish disk and numerous small spines on the top; an inner layer of smooth, six-holed buttons, with large holes. 9. *Holothuria impatiens* (Forskål), p. 393
10. Elongate, cigar-shaped body, with small terminal tentacles. No strong warts; skin fairly smooth to the touch. Spicules few delicate tables and small, smooth buttons with six holes, usually small. 10. *Holothuria arenicola* Semper, p. 393
10. Not elongate, cigar-shaped body. Skin rigid with spicules 11

11. More or less barrel-shaped with large appendages, mostly with conical base; color dark brown and yellowish, mixed. Spicules reduced tables of different size; in base of feet often enormous tables with tapering conical spire.
11. *Holothuria princeps* Selenka, p. 393
11. Flattened forms with blunt ends and small appendages; color grayish or whitish 12
12. Crowded layer of complicated tables, often with spire transformed into a hemispherical reticulum. Buttons in dorsal layer short, knobbed buttons with three pairs of holes; in ventral layer mostly longer ones with four to six pairs of holes and surface knobbed to almost smooth ..... 12. *Holothuria cubana* Ludwig, p. 394
12. Tables fairly simple; disk often partly reduced, as also the spire may be. Buttons of varying length, intermingled, with three to seven pairs of holes, with knobbed to undulating surface, often the middle bar projecting.
13. *Holothuria pseudofossor* Deichmann, p. 394

1 *Holothuria lentiginosa* v. Marenzeller

Holothuria lentiginosa v. Marenzeller, 1893a, p. 6, pl. 1, fig. 1; Deichmann, 1940, p. 196, pl. 33, figs. 1–7.

Diagnosis.—Up to 46 cm. long in life; cylindrical with 20 ventral tentacles; feet ventrally scattered, cylindrical, retractile, dorsally as contractile papillae. Color light brown, paler ventrally; tip of appendages darker, often with a paler area around the base of the papillae. Spicules tables of varying size and narrow buttons often twisted and incomplete, smooth with an occasional knob. Type: Monaco. Type locality: Off the Azores. Distribution: Eastern Atlantic, 67 to 180 fathoms and recently reported by the *Atlantis* from the south and north coast of Cuba, 175 to 255 fathoms. As a single large specimen has been taken along the northern coast of Cuba the chances are that the species belongs to the fauna of the southern part of the Gulf.

2 *Holothuria occidentalis* Ludwig

Holothuria occidentalis Ludwig, 1875, p. 104, fig. 35; Deichmann, 1930, p. 60, pl. 2, figs. 9–17; 1940, p. 197, pl. 33, figs. 8–13.

Diagnosis.—Preserved specimens up to 15 cm. long; 20 small ventral tentacles, feet tapering but with cylindrical tips on ventrum; laterally and dorsally as conical papillae. Color light brown, paler beneath, dorsal papillae almost white. Spicules small tables often with partly resorbed spire; inner layer of knobbed buttons often with holes obliterated. Type: Hamburg. Type locality: "West Indies." Distribution: Known from deeper water in the West Indies; Virgin Islands (Th. Mortensen); Old Bahamas Channel and Santarin Channel, northern Cuba (*Atlantis*). From 180 to 250 fathoms. So far the species has been reported just on the edge of the Gulf, but the chances are that it will prove to extend farther in along the northern coast of Cuba and probably along the coast of Yucatán.

3 *Holothuria glaberrima* Selenka

Holothuria glaberrima Selenka, 1867, p. 328, pl. 18, figs. 57–58; Deichmann, 1930, p. 69, pl. 4, figs. 10–13.

Diagnosis.—Up to 10 to 15 cm. long, short barrel-shaped, with large, unusually branched tentacles; numerous ventral feet; dorsally scattered papillae; soft-skinned; color black or brownish. Spicules few curved or straight rods with branched ends. Type: Museum of Comparative Zoology. Type locality: Bahamas. Distribution: Widespread in the West Indies but no definite record of its occurrence in the Gulf. The only observation about its mode of life is that of W. K. Fisher who notes "it clings to the outer side of the surf-washed rocks, usually where a tough kelp is growing." The almost dendritic, bushy tentacles indicate an adaptation for plankton feeding similar to that which characterizes the dendrochirotes.

4 *Holothuria mexicana* Ludwig

FIG. 66:20-22

Holothuria mexicana Ludwig, 1875, p. 101; Deichmann, 1926, p. 16; 1930, p. 74, pl. 5, figs. 15–20.

Diagnosis.—Huge form, 50 cm. or more when alive, thick-skinned, cylindrical, with blunt ends, ventral feet cylindrical, often completely retracted, dorsal side with insignificant papillae. Spicules scattered small tables and an inner layer of minute plates, mostly with several minute holes, resembling crackers. Color normally a dark brown or black upper side with pinkish under side; sometimes spotted, with ventral dark spots and paler dorsum, etc. Type: Hamburg (immature specimen). Type locality: Gulf of Mexico. Distribution: Common in shallow water along the lagoons of northern Cuba, also taken at Jamaica and Puerto Rico, Barbados, and as far west as Curacao. Not reported in the western part of the Caribbean nor in the Gulf. Taken occasionally in "Florida" and in the Bahamas.

Prefers sheltered eelgrass patches and similar localities.

As so often the case the young ones are seldom collected so we may assume that they live in deeper water or in crevices until they suddenly appear, almost full-grown, at a few feet of depth.

Edwards considers it the mature stage of *H. floridana* which has a similar anatomy and somewhat simpler spicules of about the same size If he is right the name must of course be withdrawn under Pourtalès' older name, but in my opinion it has a different distribution which only overlaps that of *floridana* in Florida, and there we do not know whether specimens with different types of spicules have been collected in the same spots.

5 *Holothuria floridana* Pourtalès

FIG. 66: 23

Holothuria floridana Pourtalès, 1851, p. 8; Deichmann, 1930, p. 72, pl. 5, figs. 5–9.

Diagnosis.—Medium-sized form; preserved specimens 15 cm. long; mouth slightly ventral bent with 20 large tentacles; numerous cylindrical feet on ventrum; dorsal side with low conical warts ending in small papillae. Spicules tables and numerous simple rosettes which never seem to form plates with complete holes. Color dirty white, with darker spots, sometimes uniformly dark. Type: Probably not preserved. Type locality: Florida reefs. Distribution: Extremely common in Florida as well as around Yucatán from where it was described under different names by Ives in 1890. Also reported from Swan Island and as far south as Colon, Panama, but has apparently never been taken in the waters of the Lesser Antilles or South America. A single record from northern Cuba. The adult lives freely exposed in tide pools, at utmost with a few algae or a little sand attached to the back, while the young individuals conceal themselves among mangroves or under rocks, as Pourtalès observed.

Edwards (1905, 1908) studied the early development of this form and made an attempt to correlate the growth of the animals with the changes of the spicules. He considered *H. mexicana* the aged stage of this species, but from study of his material in the United States National Museum I am inclined to disagree, although it would be tempting to take the easy course and lump the two forms. As far as I can see they have a different range which only overlaps in few places and even there we do not know whether they live in exactly the same environment. It is a question which should be attacked on the basis of freshly collected material by a modern worker, without the use of old material which possibly may have been wrongly labeled.

[6 *Holothuria grisea* Selenka

Holothuria grisea Selenka, 1867, p. 328, pl. 18, figs. 52–56; Deichmann, 1926, p. 15; 1930, p. 76, pl. 5, figs. 1–4.

Diagnosis.—Up to 25 cm. long with 20 to 25 tentacles which are downward directed; ventrally numerous soft feet, dorsally 4 to 6 rows of distinct warts, ending in papillae. Spicules, scattered tables and heaps of small plates with 2 to 4 large central holes, a few small holes in the ends and a margin with blunt teeth. Color in alcohol, salt and pepper gray; in life, with specks of bright yellow, red and black. Type: Museum of Comparative Zoology. Type locality: Haiti. Distribution: Known from Haiti, Puerto Rico, and southward along the Lesser Antilles to Rio de Janeiro, Brazil. Also reaching Colon, Panama. A single doubtful record from Florida (Sluiter's *grisea* from that region is at least partly *floridana*). Most likely this species will not be found in the Gulf although it may have been able to penetrate from south along the coasts of Central America and Mexico. It is chiefly included here to prevent misidentification.]

7 *Holothuria parvula* (Selenka)

FIG. 66: 12-13

Mülleria parvula Selenka, 1867, p. 314, pl. 38, figs. 17–18.

Holothuria parvula Deichmann, 1930, p. 70, pl. 4, figs. 14–22.

Diagnosis.—Small form, 6 to 7 cm. long, flattened with 20 large ventral tentacles, numerous ventral feet and low warts with papillae on the dorsum. Color yellowish brown, contains a greenish pigment, extracted in alcohol. Spicules a uniform layer of tables with rounded disk and squat spire and inner layer of thin, smooth elliptical buttons with two rows of small holes. Type: Museum of Comparative Zoology. Type locality: Florida. Distribution: Seems widespread in the West Indies and Bermuda, but the exact range is not known. The species occurs often in large numbers under flat rocks in tide pools. Transversal fission seems to be a normal occurrence.

As it is not uncommon in Florida it will probably also be found in Yucatán.

8 *Holothuria surinamensis* Ludwig

Holothuria surinamensis Ludwig, 1875, p. 111, fig. 37; Deichmann, 1930, p. 63, pl. 3, figs. 12–15, 19.

Diagnosis.—Up to 20 cm. long, cylindrical or slightly broader posteriorly, with 20 small terminal tentacles and few, scattered tube feet, more papilliform on the dorsal side. Color chocolate brown, often faded; tentacles yellow; skin contains a greenish pigment, soluble in alcohol. Spicules a close layer of tables with reduced disk (except in young individuals); spire with four slender rods, ending in four erect spines and four double pairs, forming a Maltese cross. Large flattened bars with dentate or perforated margin below the tables, especially numerous near the appendages. Type: Würzburg. Type locality: Surinam. Distribution: Ranges from Surinam southward to Port Seguro, Brazil, and northward to Barbados and Jamaica; common in Bermuda. Also taken at Cape Florida and other localities in "Florida," including Biscayne Bay. Like *H. parvula* it occurs in large numbers under flat rocks, and it divides also quite normally by transverse fission.

9 *Holothuria impatiens* (Forskål)

FIG. 66: 9–11

Fistularia impatiens Forskål, 1775, p. 121, pl. 39, fig. B.
Holothuria impatiens Deichmann, 1930, p. 64, pl. 3, figs. 17–18.

Diagnosis.—Up to 15 to 20 cm. long; shape similar to that of *H. surinamensis* but more warty and rougher to the touch; color various shades of gray and brown. Spicules, a uniform layer of tables with almost squarish disk with eight large marginal holes and squat spire with numerous teeth on top, and an inner layer of buttons with three pairs of large holes. Type: Undoubtedly lost. Type locality: Suez. Distribution: Almost circumtropical. Common in the West Indies and recently reported from Bermuda (Clark, 1942). A few specimens taken at low tide but apparently most specimens live concealed among rocks a little deeper than most collectors are able to reach. There are few records from Florida probably due to the difficulty in earlier times to collect below low tide. One would, however, expect that it does occur in the Gulf, especially in the part where there are coral reefs.

10 *Holothuria arenicola* Semper

FIG. 66: 14–17

Holothuria arenicola Semper, 1868, p. 61, pl. 20, pl. 30, fig. 13, pl. 31, fig. 4; Deichmann, 1930, p. 66, pl. 4, figs. 1–9.

Diagnosis.—Up to 20 cm. long, cigar-shaped or curved, with 20 small terminal tentacles and scattered small cylindrical tube feet, dorsally and ventrally. Color variable, mostly grayish with two dorsal rows of dark patches; occasionally uniformly colored or dark rusty or blackish, possibly due to external conditions. Spicules, a scattered layer of small tables and an inner layer of small oval buttons with six holes, usually small. Type: Possibly in Germany. Type locality: Bohol, Philippines. Distribution: Almost circumtropical; in the western Atlantic it ranges from Bahia, Brazil, to Bermuda, including the Lesser Antilles and Jamaica. From Florida it is known from Cape Florida and Tortugas. Normally, this species is found buried in sand or mud, but it may possibly also hide among stones. With the modern, more intensive methods of collecting with digging and sifting, it will probably prove to be much more common than hitherto assumed.

11 *Holothuria princeps* Selenka

Holothuria princeps Selenka, 1867, p. 332, pl. 18, figs. 67–69; Deichmann, 1930, p. 58, pl. 2, figs. 1–8.
Holothuria imperator Deichmann, 1930, p. 62, pl. 3, figs. 1–11.

Diagnosis.—Large forms, 20 to 30 cm. or more, often contracted to short thick-skinned barrels. Tentacles small, terminal; tube feet scattered over the entire surface, often with a conical base and ventrally ending in a cylindrical part, dorsally in a papilla. Color different shades of brown and dark yellow, often with a lighter ring around the base of the appendage. Spicules small tables more or less defect and in some individuals a few huge tables in the base of the appendages with conical spire which projects through the skin. An inner layer of irregular buttons, often incomplete with three or more pairs of holes and irregularly knobbed surface. Type: Museum of Comparative Zoology. Type locality: Florida. Distribution: As far as known only reported from the western coast of Florida and San Domingo and Yucatán; from the latter region described as *H. imperator*. The six specimens from Yucatán upon which *H. imperator* was established were only slightly larger than the types of *princeps* so a com-

parison seemed justified, but having learned how unreliable are such striking characters as the huge tack-like tables in the skin, I feel that the Yucatán species must be withdrawn as a possibly slightly older stage of Selenka's *princeps*, one in which the large, tack-like spicules have completely disappeared.

12 *Holothuria cubana* Ludwig

FIG. 66: 24–28

Holothuria cubana Ludwig, 1875, p. 104, pl. 7, fig. 34; Deichmann, 1930, p. 54, pl. 1, figs. 1–8.

Diagnosis.—Up to 15 cm. long, flattened with blunt ends, ventral mouth with 20 small tentacles. Tube feet ventrally small and scattered, often retracted into pits, dorsally few and papilliform. Color white or gray. Spicules a crowded layer of tables with knobbed disk and spire gradually transformed into a reticulated hemisphere. Inner layer of knobbed buttons, short, strongly knobbed with three pairs of holes on the dorsal side; ventrally mostly larger with four to six pairs of holes and less strongly knobbed, sometimes almost smooth. Type: Vienna. Type locality: Off Cuba. Distribution: Reported from the West Indies from Florida, Curaçao, Barbados, and Bermuda. This burrowing form should find excellent conditions in the sandy flats in the Gulf of Mexico.

13 *Holothuria pseudofossor* Deichmann

FIG. 66: 29–30

Holothuria pseudofossor Deichmann, 1930, p. 57, pl. 1 figs. 9–14.

Diagnosis.—Resembles *H. cubana* but has larger appendages and these are more inclined to remain expanded. The spicules are regular tables with eight marginal holes, more or less knobbed edge and low spire with numerous teeth. The buttons have three to seven pairs of holes and large and small ones are found intermingled; the surface is knobbed to smooth. Type: Museum of Comparative Zoology. Type locality: Montego Bay, Jamaica. Distribution: So far known only from the type locality where it is fairly common, buried in sand under slabs of coral rocks.

Order 3 DENDROCHIROTA Grube

KEY TO THE FAMILIES KNOWN FROM THE GULF OF MEXICO

1. Part of the ventral side developed as a sole, while the remaining part of the body is covered by scales..2. Psolidae, p. 401
1. Part of the ventral side not set off as a sole..2
2. Tentacles 10, often the 2 ventral smaller. (In some deep water forms the number reduced to 8, and the tentacles almost unbranched.)..1. Cucumariidae, p. 394
2. Tentacles 20, in 2 more or less distinct circles..3. Phyllophoridae, p. 402

1 Cucumariidae

KEY TO THE GENERA KNOWN FROM THE GULF OF MEXICO

1. Shallow water forms..2
1. Deep water forms (at least around 100 fathoms depth). Body covered by large circular scales..8
2. Calcareous ring tubular, with distinct tails..3
2. Calcareous ring simple, or with short posterior prolongation..6
3. Spicules predominantly elongate plates with a varying number of holes, usually in two rows. Feet scattered over the entire surface in the adult animals..4. *Thyoneria* nom. nov., p. 398
3. Spicules not predominantly elongate plates..4
4. Spicules four-holed buttons, forming a crowded layer in the skin..3. *Neothyone* Deichmann, p. 397
4. Spicules tables with four to eight holes in disk and two to four-pillared spire; spicules in some forms reduced with age..5
5. Tube feet in five crowded bands..1. *Pentamera* Ayres, p. 395
5. Tube feet scattered over entire surface of body, except in very young individuals..2. *Thyone* Oken s. str., p. 395
6. Dorsal side with large warts; ventral tube feet in three broad bands; short, box-like form, chocolate brown
7. *Pentacta* Goldfuss, p. 399
6. Dorsal side not with large warts..7
7. Ring low, simple. Spicules regularly knobbed buttons and an outer layer of deep baskets with a wreath of short spines along the rim. Stout, barrel-shaped or lemon-shaped form with thick skin, large oral valves and tube feet scattered over the body..6. *Euthyonacta* nom. nov., p. 399
7. Ring simple or with short posterior prolongations. Spicules mostly knobbed buttons, irregular or regular.
5. *Thyonella* Verrill, p. 399
8. Plates with excentric spire..8. *Echinocucumis* Sars, p. 400
8. Plates with centrally placed spire or spine..9. *Sphaerothuria* Ludwig, p. 400

Genus 1 PENTAMERA Ayres 1852

Pentamera pulcherrima Ayres

Pentamera pulcherrima Ayres, 1854, p. 200; Deichmann, 1941, p. 84.

Diagnosis.—Small species, at utmost 10 cm. long. Ovoid, with oral and anal ends upward curved. Feet in five crowded bands. Color white or dirty brown with tentacles dotted with dark pigment. Spicules two-pillared tables with oval disk with four holes. Feet with large end plate and curved supporting tables with two-pillared spire, sometimes reduced. Type: Undoubtedly lost. Type locality: Charleston, S. C. Distribution: Common along the Atlantic seaboard, occasionally reaching the coasts of New England. Taken at Sabanilla, Columbia (U. S. National Museum), and once reported from the coast of Texas (J. Hedgpeth, letter). In the South it is taken in shallow water where it lives buried in the mud. In the northern waters it lives in deeper water and is either washed up after storms or dredged. Grave (1905) has reared it from eggs taken with free swimming larvae in the plankton around Beaufort, N. C. Some of these specimens were kept alive for 3 years.

Genus 2 THYONE Oken 1815

KEY TO THE SPECIES KNOWN FROM THE GULF OF MEXICO

1. Spicules in skin tables with large disk; supporting tables in feet with enormous, reticulated spire. Apparently spicules preserved throughout the animal's life ..... 1. *Thyone mexicana* Deichmann, p. 395
1. Spicules in skin tables with disk of normal size; supporting tables with normal spire, or a low reticulum 2
2. Disk of tables thick, oval, with four small holes; spire two-pillared with two large clusters of spines; sometimes a handle is present on the other side of the disk making a transition to the buttons found in other genera. 2. *Thyone pseudofusus* Deichmann, p. 395
2. Disk of tables of normal thickness, with four large and up to four smaller marginal holes. Spire often delicate with feeble spines 3
3. Tables usually with squarish disk, and tendency to have four pillars in the spire; supporting tables with complex, low spire. Large species, 12 cm. or more; greenish or brownish ..... 3. *Thyone briareus* (LeSueur), p. 395
3. Tables oval or squarish, with weakly developed two-pillared spire. Supporting tables delicate. Seems never to attain its full size in American waters. Possibly a guest from the eastern Atlantic ..... 4. *Thyone inermis* Heller, p. 397

1 *Thyone mexicana* Deichmann

FIG. 67: 1-3

Thyone mexicana Deichmann, 1946, p. 1, text fig. 1.

Diagnosis.—Large form 10 cm. or more; resembles the type species *T. fusus* from the northeastern Atlantic, but the spicules appear to be retained throughout life and the feet are more clumsy on account of the tall, thimble-shaped spire on the supporting tables. Color mottled brown. Spicules tables with several circles of holes and knobbed edge; spire with two pillars and occasionally three to four. Feet with end plate and numerous supporting tables with huge, reticulated spire. Type: U. S. National Museum. Type locality: Sugarhouse Bend, Barataria Bay, Grand Isle, Louisiana. Distribution: So far known from the coast of Louisiana and Texas, in tidepools, down to few fathoms.

2 *Thyone pseudofusus* Deichmann

Thyone pseudofusus Deichmann, 1930, p. 168, pl. 14, figs. 6–9; 1941, p. 107.

Diagnosis.—Small species 4 to 5 cm. long. Spicules tables with oval disk with thick rim, two-pillared spire with clusters of spines on top and frequently a handle on the inner side. Type: U. S. National Museum. Type locality: Yucatán, 25 fathoms. Distribution: Known from Yucatán, Florida, Tobago, British West Indies, and coast of Brazil. In Yucatán 18 specimens were taken in the same haul so the species may possibly have direct development with the larvae settling down close to the parents.

3 *Thyone briareus* (LeSueur)

Holothuria briareus LeSueur, 1824, p. 161.

Thyone briareus Deichmann, 1930, p. 165, pl. 13, figs. 5–7; 1938, p. 134; 1946, p. 3.

Diagnosis.—Large robust form, 12 cm. or more, with numerous tube feet which give an almost hairy aspect to the animal. Skin soft due to the scarcity of spicules; color dark greenish or brown; sometimes faded in alcohol. Spicules scattered tables with mostly squarish disk; often three to four pillars in spire; feet with large end plate and elongate supporting tables with low irregular spire composed of several rods. Type: Lost. Type locality: Florida. Distribution: From

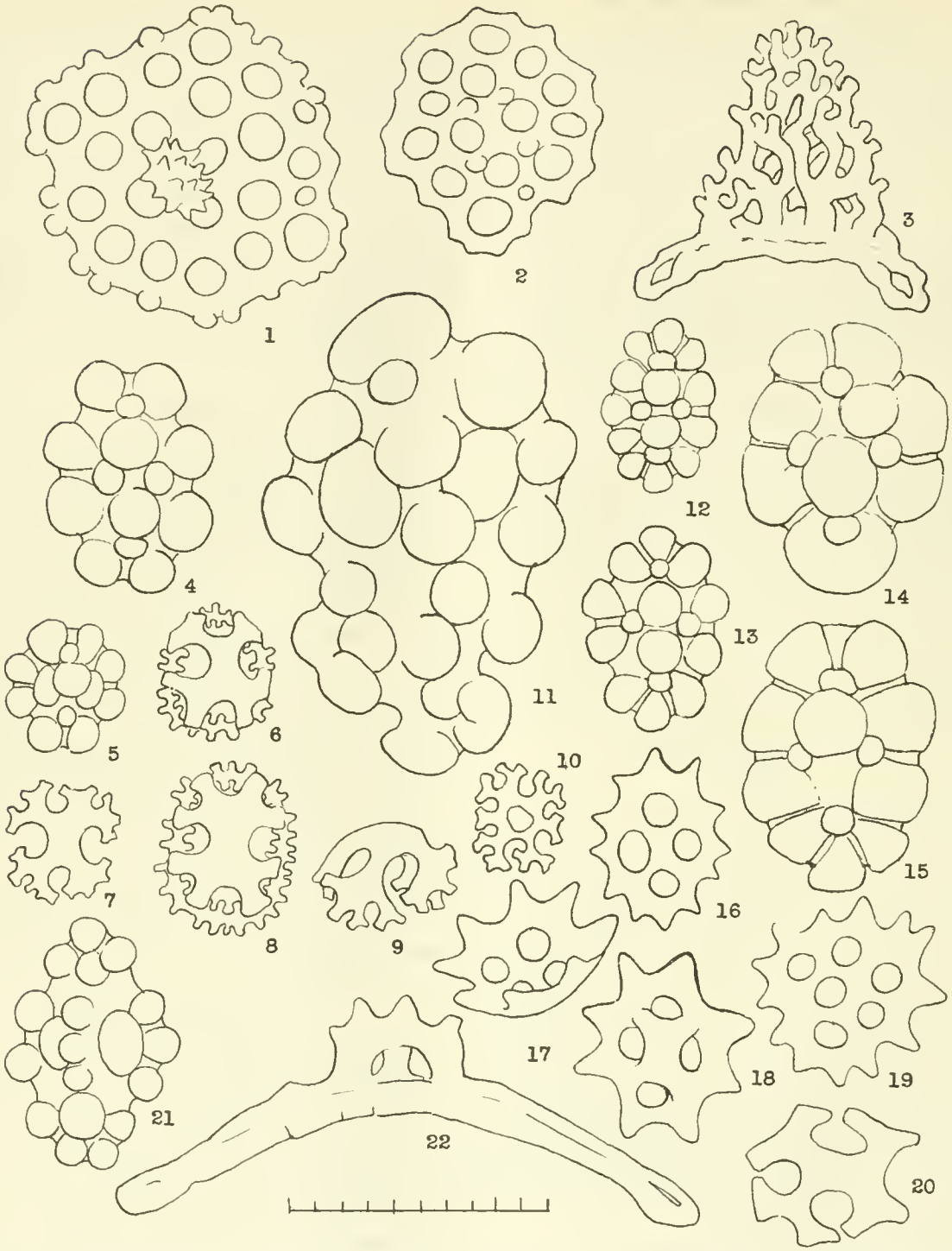

FIGURE 67: 1–20.—*Thyone mexicana* Deichmann, p. 395. 1–2, disk of tables from body wall; 3, supporting table from tube foot, side view. *Pentacta pygmaeus* (Théel), p. 399. 4–5, knobbed buttons; 6–9, baskets from outer layer of skin; 10, perforated plate; 11, knobbed plate. *Thyonella pervicax* (Théel), p. 399. 12–15, knobbed buttons; 16–20, baskets from outer layer of skin. *Neothyone belli* (Ludwig), p. 397. 21, knobbed button with knobbed handle; 22, supporting table from tube foot. Magnification: ×400 Division 1/100 mm.

Texas to Florida and northward along the Atlantic seaboard to Woods Hole, Mass. Shore to few fathoms depth, in muddy localities, often attached to eelgrass in muddy sheltered localities. At Cocoplum Beach in Biscayne Bay, H. L. Clark dug it out of the mud in the same localities as *Leptosynapta micropatina* while in Woods Hole the year-old individuals were picked off the eelgrass.

The species has been extensively used for experimental work at Woods Hole and may possibly be even more useful in the South where many animals are more tolerant to warm water than they are in the North.

In Woods Hole, *T. briareus* breeds in June–July but very likely the season is earlier in the Gulf and around Florida. The eggs are small and develop in 3½ days (Ohshima 1925) into a creeping larva which soon acquires tentacles and after 3 months is completely equipped with spicules of the same type as in the adult though naturally scaled down to the size of the few millimeter long specimens. In June, the following year, the smallest individuals found measure 2 cm. in length with no trace of genital organs. In specimens 3 to 4 cm. long gonads are present and increase the following years in length and number of the tubes. After 5 years the animals are ready to spawn, but whether they die after the spawning or regenerate the gonads is not known. The spawning has been studied by Colwin (1948).

Kille has studied the regeneration of the tentacles which is accomplished in 3 weeks. Extirpated gonads regenerate very fast if small pockets of germ cells are left; if completely removed it will take several months before the glands stage a comeback.

It is one of the few species which as far as known has no parallel form in the Panamic region. Troschel had apparently some mislabeled *Thyone briareus* which he described as *Anaperus peruviana* (Lesson), a deep purple form with simple calcareous ring. As the Panamic region recently has been rather thoroughly explored by the Hancock Expeditions it seems rather unlikely that so large a species as one resembling *T. briareus* could have escaped attention.

Thyone inermis Heller

Thyone inermis Heller, 1868, p. 78; Deichmann, 1947, p. 84, pl. 1, figs. 7–13; pl. 2, figs. 1–17.

From Tobago, British West Indies, and Florida has occasionally been reported a small species which, with some doubt, has been referred to *T. fusus* (O. F. Müller), the well-known type species from the northeastern Atlantic. It appears, however, that one has been dealing with a southern species typical of the Mediterranean and the waters around Portugal, the Azores, as far north as Roscoff, France.

As the American material always has been immature, few centimeters long, it seems likely that the species appears intermittently only and has been unable to be established in the western Atlantic. It is included here because a somewhat similar form is known from the Panamic region, and if it has a parallel form in the Caribbean and the Gulf one might be inclined to identify it with the European invader which most likely does not extend its range into the Gulf.

Genus 3 NEOTHYONE Deichmann

Neothyone Deichmann, 1941, p. 106; new name for Selenka's *Stolus gibber*, 1867, p. 356 and allied forms.

Remarks.—In the Panamic region three species have been referred to this genus. In the West Indian region only one species is known, previously listed under three different names.

Neothyone belli (Ludwig)

FIG. 67: 21–22

Thyone belli Ludwig, 1887, p. 21, pl. 1, figs. 10–13; Deichmann, 1930, p. 176, pl. 14, figs. 10–13.

Thyone micropunctata Sluiter, 1910, p. 338, text fig. D a-c; Deichmann, 1930, p. 171, pl. 14, figs. 14–18.

Cucumaria argillacea Sluiter, 1910, p. 336, text fig. B a-c; Deichmann, 1930, p. 160 (not examined).

Diagnosis.—Small form, 5 cm. long, with skin rigid from the numerous spicules. Color dirty gray, sprinkled with dark spots. Spicules knobbed buttons with six marginal knobs and two central, often fused to a handle. Type: Würzburg; Sluiter's type may be in Germany. Type locality: Abrolhos Reefs, Bahia, Brazil; Sluiter's types came from Tortugas, Florida. Distribution: From Abrolhos Reef, Brazil, to Colon Harbor, Panama, including Trinidad and Tobago. Also taken at Tortugas. Shore to 12 fathoms.

Reexamination of the available material of *T. belli* and *T. micropunctata* has convinced me that the two species cannot be kept separate, and undoubtedly Sluiter's 8 mm. long *C. argillacea*, taken at the same locality as his *micropunctata* is the young of the latter. The differences in the calcareous ring which his figures indicate are such

as is often observed in material of different age. More surprising is his statement that *argillacea* possessed small gonads, but he may have mistaken some lobes of the respiratory trees for these organs.

Genus 4 THYONERIA nom. nov.

New name for *Semperia cognata* Lampert 1885.

Thyoneria cognata (Lampert)

Semperia cognata Lampert, 1885, p. 67.
Thyone cognita Deichmann, 1930, p. 169, pl. 15, figs. 1–4.
Thyone cognata H. L. Clark, 1933, p. 115. Deichmann, 1938c, p 134.

Diagnosis.—Large form, 14 cm. long, fairly delicate, spindle-shaped, often oral and anal ends turned up. Tentacles 10, of equal size. Feet in double rows and scattered interambulacrally. Calcareous ring tubular, with distinct tails and tall, narrow interradials. Spicules numerous elongate plates with mostly two rows of holes and a varying number of smaller, button-like holes with up to four holes. End plate in feet small, almost rudimentary except in young individuals; walls of feet with perforated rods, with or without a third arm. Introvert with rosettes; tentacles with heavy rods in stem and delicate ones in the terminal branches. Type: Possibly in Germany. Type locality: Fernando do Noronhas, Cuba. Distribution: Cuba, Yucatán, Tortugas, and Biscayne Bay, Florida. Shallow water down to few fathoms depth. H. L. Clark reports it at Biscayne Bay, from soft bottom in patches of eelgrass.

Genus 5 THYONELLA Verrill 1872

Remarks.—The genus was established, rather casually, by Verrill for Pourtalès' *Colochirus gemmata*. The name has been discarded by most authors, but it seems to be the only one suitable for *gemmata*. The diagnosis has been enlarged so it takes in the members of *Thyonacta* Deichmann and provisionally Théel's *Thyone pervicax* which has become homeless after the name *Thyone* has been restricted to the species with delicate tables in the skin.

KEY TO THE SPECIES OF THYONELLA KNOWN FROM THE GULF OF MEXICO

1. Tube feet numerous, covering the entire body as slightly conical warts. Small form, 7 cm. long; curved, rigid body. Color white with brown spots, or light brown ..... 3. *Thyonella pervicax* (Théel), p. 399
1. Tube feet in distinct double rows along the ambulacra, and scattered in the interambulacra but not covering the surface uniformly. Large forms, 15 cm. long. Color mottled gray or brown 2
2. Cups in outer layer star-shaped, with four central holes and eight large marginal teeth. Mottled gray ..... 1. *Thyonella gemmata* (Pourtalès), p. 398
2. Cups in outer layer ring-shaped, with four small marginal holes in the corners; marginal teeth small and blunt. Uniformly grayish brown ..... 2. *Thyonella sabanillensis* (Deichmann), p. 399

1 *Thyonella gemmata* (Pourtalès)

Colochirus gemmata Pourtalès, 1851, p. 11.
Thyone gemmata Deichmann, 1930, p. 177, pl. 17, figs. 1–3.

Diagnosis.—Large species, 15 cm., spindle-shaped, often somewhat curved; feet in double rows along the ambulacra and scattered in the interambulacra, cylindrical except toward the ends where they tend to become papilliform. Color brownish-grayish mottled. Spicules externally flattened baskets with eight broad teeth and four central holes; an inner layer of four-holed buttons more or less regular and knobbed, with tendency to become more irregular with age, with holes reduced and surface undulated. Feet apparently without end plate; walls stiffened by thick perforated rods; in papillae triangular plates or short tri-armed rods. Introvert with rosettes, and small spectacle-shaped rods. Tentacles with heavy rods with small holes. Type: Undoubtedly lost. Type locality: Sullivan Island, S. C. Distribution: Like *Thyone briareus* it seems to be one of these species which is restricted to the Gulf of Mexico and the Atlantic seaboard. It is known from Yucatán, Texas, Florida, and South Carolina. Also reported from near Woods Hole but seems not to be permanently established so far north. As far as known, always dredged from a few fathoms depth.

The records from Maine and Barbados are omitted as they undoubtedly refer to individuals which have been mislabeled. The species appears to live buried in mud, and it is apparently one of the most common species in the Gulf. Like so many other of the larger species it is practically unknown as young. The smallest individuals I have seen measured 4 cm. in length but in strongly contracted condition.

2 *Thyonella sabanillensis* (Deichmann)

Thyone sabanillensis Deichmann, 1930, p. 178, pl. 17, figs. 4–19.

Thyonacta sabanillensis Deichmann, 1941, p. 101.

Diagnosis.—Large form, 15 cm. Resembles a somewhat more delicate *T. gemmata*, with stronger tendency to papillae toward the ends of the body and dorsally. Color uniformly grayish brown. Spicules an external layer of flattened baskets with uneven margin with blunt teeth and four small accessory holes besides the four central ones. Inner layer buttons with strongly knobbed surface and irregular plates with undulating to smooth surface. Feet without end plate, walls with curved thick supporting rods with small holes. In papillae often triangular plates, more or less strongly bent. Introvert with rosettes; tentacles with perforated rods which decrease in size toward the tips. Type: United States National Museum. Type locality: Sabanilla, Columbia, shallow water. Distribution: So far known only from the type locality and the western part of the Gulf of Mexico, coast of Texas (Hedgpeth). Few fathoms depth.

3 *Thyonella pervicax* (Théel)

FIG. 67: 12–20

Thyone pervicax Théel, 1886a, p. 93, pl. 5, fig. 9; pl. 2, fig. 3; Deichmann, 1930, p. 175, pl. 16, figs. 9–12.

Diagnosis.—Medium sized form, 7 cm. long, with rigid skin; ventral tentacles small; tube feet with conical base, covering the surface completely even in small individuals, at utmost with a faint indication of serial arrangement along the ambulacra. Color white or pale brown, sometimes with brown spots. Spicules an external layer of flattened cups with large marginal spines; an inner layer of four-holed, strongly knobbed buttons of two sizes. Feet with small end plate or none and walls stiffened by slightly curved rods, spectacle-shaped with one or more holes in each end. Type: British Museum. Type locality: Bahia, Brazil. Distribution: Reported from the type locality, Tortugas, and other localities on the Gulf side of Florida. Occasionally dredged in Vineyard Sound. Seems always to be taken at some fathoms depth. Although the species has spicules somewhat similar to *gemmata* they are nevertheless sufficiently different to prevent misidentification. Aside from the differences in the calcareous ring *pervicax* has more feet even at an early stage than has *gemmata* and the latter is also more darkly colored. It is evidently one of the most common species off the west coast of Florida.

Genus 6 EUTHYONACTA nom. nov.

New name for *Thyone solida* (Deichmann).

Euthyonacta solida Deichmann

Thyone solida Deichmann, 1930, p. 172, pl. 15, figs. 11–17, pl. 16, figs. 1–2.

Diagnosis.—Heavily built, thick-skinned form with barrel-shaped body, five heavy oral valves and tube feet scattered uniformly over the body, more papilliform on the dorsum and at the ends. Color in alcohol yellowish brown. Simple ring. Spicules an outer layer of deep baskets with a wreath of teeth along the rim and an inner layer of regularly knobbed buttons of varying size. Feet apparently without end plate, though a number of branched rods may substitute for such one; walls packed with heavy rods, often with a third arm. Introvert with rosettes and small buttons with almost smooth surface. Tentacles with strong, perforated rods, decreasing in size toward the tips. Type: United States National Museum. Type locality: Gulf of Mexico, *Albatross* station 2369. Distribution: So far known only from the Gulf of Mexico from 26 to 30 fathoms depth. The largest individuals examined were about 6 cm. long with the tentacles retracted. From the size of the gonads I judge that the species may reach a much larger size, 15 to 20 cm. or thereabout. It was taken from coarse gray sand and broken corals in which it most likely lives concealed.

Genus 7 PENTACTA Goldfuss 1820

Pentacta pygmaea (Theel)

FIG. 67: 4–11

Colochirus pygmaeus Théel, 1886, p. 92, pl. 4, fig. 9.

Pentacta pygmaea, Deichmann, 1930, p. 180, pl. 21, figs. 10–16.

Diagnosis.—Medium-sized form, 7 cm. long, with short, box-like body, with cylindrical feet in three bands on the ventrum; dorsal side with blunt papillae along the ambulacra with some tendency to spread out into the interambulacra. Strong oral valves with papillae. Color chocolate brown, paler below. Spicules an external layer of deep baskets often with rim incomplete; an inner layer of strongly knobbed four-holed buttons with 10 knobs besides a varying number of much

smaller buttons with a larger number of knobs. Also scattered perforated plates with flat to knobbed surface. Feet with or without a small end plate; walls with stout supporting rods, often with a third arm. In the papillae the supporting rods are modified into plates, bent or flat. Introvert with rosettes; tentacles with heavy perforated rods. Type: British Museum. Type locality: Bahia, Brazil. Distribution: Ranges from Brazil, Trinidad to Florida and South Carolina. From tide mark down to 20 fathoms. In the Mexican Gulf known from Sanibel Island, Florida. The strong development of the ventral feet indicates that the animals live, limpet-like, attached to hard bottom, and this was observed to be the case of a specimen collected at Maguerepe Bay, Trinidad. It seems to be one of the more common species along the west coast of Florida.

Genus 8 ECHINOCUCUMIS Sars 1859

Echinocucumis hispida (Barrett)

Eupyrgus hispidus Barrett, 1856, p. 46, pl. 4, figs. 1a–6.
Echinocucumis hispida, Deichmann, 1930, p. 150, pl. 18, fig. 9.

Diagnosis.—Few cm. long, globular, with anterior and posterior end drawn out into short tubes; tentacles 10, almost finger-shaped. Spicules plates with large holes, smaller toward the margin, and spire, if present, reticulated and excentric in position. The feet pass out between the plates which often are indented for their passage. Type: Probably lost. Type locality: Coast of Norway. Distribution: From North Cape to Discaya, 100 to 250 fathoms. In the western Atlantic taken by Pourtalès near Florida and also by the *Albatross* between Bahamas and Cuba at 85 to 193 fathoms depth. Apparently the species is not common in the western Atlantic.

Echinocucumis hispida (Barrett) var. *atypica* Deichmann

Echinocucumis typicus Théel, 1886a, p. 9 (partim).
Echinocucumis hispida (Barrett) var. *atypica* Deichmann, 1930, p. 152, pl. 18, figs. 10–11.

Diagnosis.—As the typical form, except the spire is solid. Type: Museum of Comparative Zoology. Type locality: Off St. Kitts, 116 fathoms. Distribution: Taken from the type locality and off Havana, 100 fathoms depth.

Genus 9 SPHAEROTHURIA Ludwig 1894

KEY TO THE SPECIES KNOWN FROM THE GULF OF MEXICO

Scales coarsely reticulated; reticulation appears late. Tentacles with perforated, oblong plates.
Sphaerothuria asperrima (Théel), p. 400

Scales finely reticulated; reticulation appears early. Tentacles with cylindrical rods.
Sphaerothuria talismani (Perrier), p. 400

Sphaerothuria asperrima (Théel)

Echinocucumis asperrima Théel, 1886a, p. 10.
Sphaerothuria asperrima Deichmann, 1930, p. 152, pl. 19, figs. 1–2.

Diagnosis.—Large species, body 2 cm. in diameter; oral and anal tubes 2 cm. (together). Scales up to 2 mm. in diameter; spire centrally placed and with several pillars. Type: Museum of Comparative Zoology. Type locality: Islas de Pinos, Cuba, 158 fathoms. Distribution: Also taken off Kingston, Jamaica, Virgin Islands, and off Morro Light, Cuba. From 24 to 400 fathoms. In the smallest specimen, from off Morro Light, the plates lack almost all reticulation, but the feet pass through the plates and the scales are also larger than in *E. hispida* which is the species one might be inclined to refer it to.

Sphaerothuria talismani (Perrier)

Ypsilothuria talismani Perrier, 1902, p. 318, pl. 12, figs. 9–10, text fig. 12.
Sphaerothuria talismani Deichmann, 1930, p. 154, pl. 19, fig. 3.

Diagnosis.—Small form with finely reticulated plates, with central spire with numerous crossbars. Tentacles with cylindrical rods with perforated ends. Type: Paris. Type locality: Cape Finis Terre, Spain. Distribution: From Biscaya to west coast of Africa, 300 to 1,000 fathoms. In the western Atlantic taken along the Lesser Antilles and north of Havana and along the coast of New England. In the eastern Atlantic taken from 300 to 1,000 fathoms (if all Perrier's material refers to the same species); in the American waters taken from 339 to 1,491 fathoms.

Family 2 PSOLIDAE

KEY TO THE GENERA KNOWN FROM THE GULF OF MEXICO OR LIKELY TO OCCUR THERE

1. Dorsal side with numerous tube feet and scales covered by a layer of complex spicules, hour-glasses, towers, curved plates, etc. ..... 1. *Thyonepsolus* H. L. Clark, p. 401
1. Dorsal side without tube feet; scales naked or covered by a varying number of grains or cups, or both 2. *Psolus* Oken, p. 401

Genus 1 THYONEPSOLUS H. L. Clark 1901

Thyonepsolus braziliensis Théel

Thyone braziliensis Théel, 1886a, p. 15, fig. 7.

Thyonepsolus braziliensis Deichmann, 1930, p. 192, pl. 21, figs. 1–6; 1937, p. 173.

Diagnosis.—Small species, few cm. long, with 7 to 10 scales between oral and anal scales. Plates in outer layer of dorsal side small, incomplete; hour-glass shaped bodies relatively simple; towers present in varying numbers, obviously a juvenile character. Plates in sole with almost smooth even margin; tentacles with delicate rods and rosettes. Type: Museum of Comparative Zoology. Type locality: Porto Seguro, Brazil. Distribution: As far as known only taken at the type locality and Tobago, British West Indies, but as it is a small inconspicuous species it may occur much more widespread. In shallow water, attached to rocks or seaweeds. Nothing is known about its life; even the color is not known though it most likely is bright red just as the closely related form known from the Panamic region. In Tobago several small individuals were taken from the same spot indicating that the development is direct, but it is doubtful whether the eggs are carried around in depressions on the mother's back as is the case in *T. nutriens* H. L. Clark, from the Californian waters.

The genus with its three species is restricted to the American waters, and the chances are that *T. braziliensis* also exists in the Gulf of Mexico.

Genus 2 PSOLUS Oken 1915

KEY TO THE SPECIES KNOWN FROM THE GULF OF MEXICO OR LIKELY TO OCCUR THERE

1. Dorsal scales covered by grains and small, regular cups. ..... [3. *P. complicatus* Deichmann, p. 402]
1. Dorsal scales covered by grains but no cups. 2
2. Few scales (2–4) between oral and anal scales. Grains few, large and ultimately fused with the scales, forming large protuberances. ..... 1. *P. tuberculosus* Théel, p. 401
2. Several scales (up to 6–7 scales) between oral and anal scales. Grains of moderate size. ..... 2. *P. operculatus* Pourtalès, p. 401

1 *Psolus tuberculosus* Théel

Psolus tuberculosus Théel, 1886a, p. 13, pl. 1, fig. 5; Deichmann, 1930, p. 186, pl. 20, fig. 3.

Diagnosis.—Small form, sole up to 3 cm. long; huge oral valves; anus surrounded by two circles of small scales; up to four scales between oral and anal scales. Feet restricted to the lateral ambulacra on the ventral sole. Spicules dorsally grains which increase enormously and finally fuse with the scales forming huge, blunt protuberances. Sole with perforated plates often two holes larger than the rest. Type: Museum of Comparative Zoology. Type locality: Sand Key, 500 fathoms. Distribution: The waters around Florida, Tortugas, and Campeche Bank, Mexico. Usually about 100 fathoms (95–135 fathoms); the type appears to have come from exceptionally deep water. The species is closely related to Fisher's *P. macrolepis* from Hawaii and Ludwig's *P. diomedeae* from Gulf of California to Ecuador and the Galapagos Islands. (See Deichmann, 1941, p. 149.)

2 *Psolus operculatus* (Pourtalès)

Cuviera operculata Pourtalès, 1868, p. 127; 1869, p. 359, 361.

Psolus operculatus Deichmann, 1930, p. 187, pl. 20, figs. 1–2.

Diagnosis.—Small form, sole up to 4 cm. long. Resembles *P. squamata* (D. & K.) with thin, imbricating scales, distinct oral valves, and up to seven scales between oral valves and anal scales; feet along margin of sole with a few at the ends of the odd ambulacrum. Spicules dorsally grains, lacking in very young individuals. Sole with heavy, four-holed buttons, with knobbed margin, increasing in number with age. Type: Museum of Comparative Zoology. Type locality: Sand Key, Florida, 120 to 125 fathoms. Distribution:

Known from the waters around Florida and Barbados. From about 100 fathoms (103–137).

[3 ***Psolus complicatus*** **Deichmann**

Psolus operculatus Théel, 1886a, p. 9 (partim).
Psolus complicatus Deichmann, 1930, p. 185, pl. 19, figs. 6–9.

Diagnosis.—Resembles *P. operculatus* but has in addition to grains on the dorsum, deep baskets; deposits in the sole are larger knobbed buttons, often with a secondary reticulum. Type: Museum of Comparative Zoology. Type locality-Off Barbados, 137 fathoms. The species is known from the type locality only, taken in the same haul as material of *operculatus*. One almost expects that a larger series will prove that the two species must be merged.]

Family 3 PHYLLOPHORIDAE

KEY TO THE GENERA KNOWN FROM THE GULF OF MEXICO

1. Deep water forms (100–200 fathoms or more). Skin paper-thin, stiff from numerous four-pillared tables ..... 6. *Benthophyllophorus* nov. nom., p. 405
1. Shallow water forms; tide pools to few fathoms depth 2
2. Spicules perforated, knobbed plates ..... 5. *Phyllophorus* Grube,[1] p. 405
2. Spicules tables 3
3. Tables with distinctly dentate margin and low, two-pillared spire ..... 1. *Trachythyonidium* nov. nom., p. 405
3. Tables with smooth margin or slightly uneven, at utmost blunt dentate 4
4. Tables with four large holes, alternating with four small ones ..... 3. *Neophyllophorus* nom. nov., p. 404
4. Tables with 8 to 10 or more holes, in a circle or oval 5
5. Disk oval with smooth margin ..... 2. *Paraphyllophorus* nov. nom., p. 402
5. Disk circular with uneven edge, sometimes blunt dentate ..... 4. *Lipotrapeza* H. L. Clark, p. 404

Genus 1 TRACHYTHYONIDIUM nov. nom.

New name for *Thyonidium occidentale* Ludwig.[2]

Trachythyonidium occidentale **(Ludwig)**

FIG. 68: 1–5

Thyonidium occidentale Ludwig, 1875, p. 119.
Phyllophorus occidentale Deichmann, 1930, p. 148, pl. 18, figs. 1–2.
Euthyonidium occidentalis Deichmann, 1938, p. 380; 1941, p. 124.
Thyonidium constituta Sluiter, 1910, p. 340, text fig. E; Deichmann, 1926, p. 124.

Diagnosis.—Up to 10 cm. long, with five pairs of large and five pairs of small tentacles. Color dark brown to yellow. Calcareous ring short tubular, with short tails which may become almost completely reduced. Spicules tables with dentate margin on the disk and four to eight holes, and two-pillared spire with few spines, sometimes reduced to four basal teeth. Type: Possibly in Germany. Type locality: Surinam. Distribution: From Porto Seguro, Brazil, Surinam, Trinidad, Antigua to the waters around Florida. The species has been taken at Tortugas where it occurs in 3 feet of water in eelgrass patches. A closely related species is known from the Panamic region (Deichmann, 1941).

Genus 2 PARAPHYLLOPHORUS nov. nom.

New name for *Thyonidium parvum* Ludwig and related forms.

Paraphyllophorus parvus **(Ludwig)**

FIG. 68: 12–13

Thyonidium parvum Ludwig, 1881, p. 54, pl. 3, figs. 16–18; Deichmann, 1930, p. 149; 1938, p. 133, pl. 1, figs. 19–21; H. L. Clark, 1933, p. 113.

Diagnosis.—Up to 5 to 7 cm. long in preserved condition. Tentacles 20, of uneven size; the two circles not well separated. Color in life brilliant red with red or purplish tentacles; in alcohol yellowish white. Spicules numerous tables with oval to circular disk and 8 to 10 marginal holes and spire with two to four pillars ending in a cluster or wreath of spines. Type: Possibly in Germany. Type locality: Coast of Brazil. Distribution: According to Ludwig it is not uncommon along the coasts of Brazil in shallow water. It has been reported once from Antigua, British West Indies and recently from Biscayne Bay, Florida, in grassy flats. Although not yet re-

[1] The key here refers only to the West Indian representative. The type species, *P. urna* Grube, from the Mediterranean Sea, and related forms, have tables which disappear early in life. Possible the young of the West Indian species may have tables (or it may prove to be erroneously referred to the West Indian fauna).

[2] The name *Euthyonidium* Deichmann, 1938, has been withdrawn as a complete synonym of *Pentadactyla* Hutton, which has been reinstated.

ported from the Gulf, it seems most likely that it will prove to live there also.

A closely related form is known from the Panamic region (Deichmann, 1941).

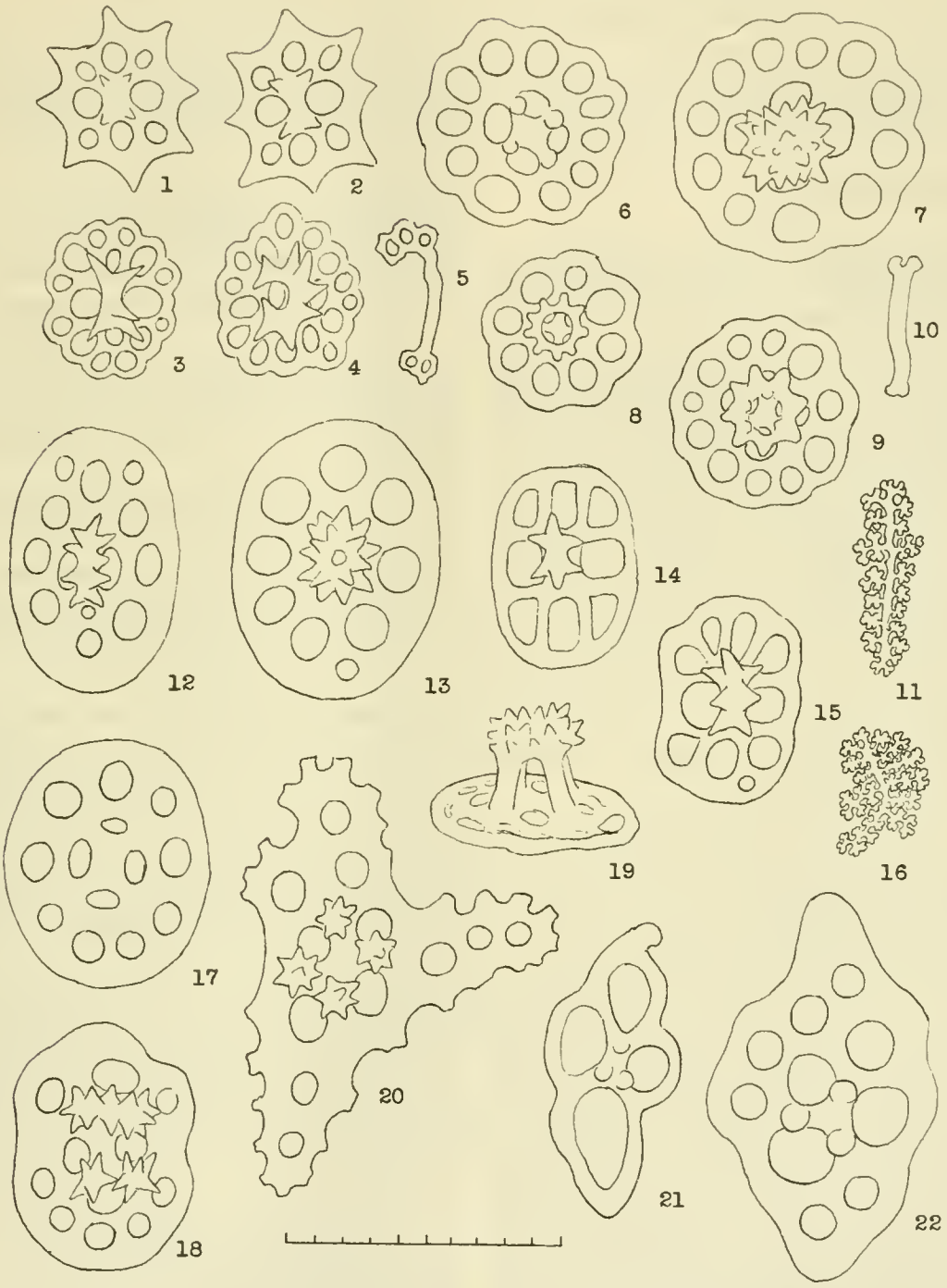

FIGURE 68: 1–22.—*Trachythyonidium occidentale* (Ludwig), p. 402. 1–2, tables from skin; 3–4, tables from introvert; 5, rod from tentacle. *Lipotrapeza seguroensis* Deichmann, p. 404. 6–9, tables from skin; 10, rod from tentacle; 11, rosette) from introvert. *Paraphyllophorus parvus* (Ludwig), p. 402. 12–13, tables from skin. *Neophyllophorus desticatus*, (Deichmann), p. 405. 14–15, tables from skin: 16, rosette from introvert. *Benthophyllophorus conchilegum* (Pourtalès) p. 405. 17–19, tables from skin; 20, table from introvert. *Molpadia cubana* Deichmann, p. 405. 21, table from skin; 22, table from tail. Magnification: ×400 Divisions 1/100 mm.

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Genus 3 NEOPHYLLOPHORUS nov. nom.

New name for *Phyllophorus zacae* Deichmann and related species.

KEY TO THE SPECIES OF NEOPHYLLOPHORUS

Tables with oral disk, with smooth edge and four squarish holes and four smaller wedge-shaped ones. Spire with two pillars and few teeth. ..... 1. *Neophyllophorus destichadus* (Deichmann)

Tables with oval to rectangular disk with four large holes and four smaller ones. Spire sometimes reduced to two knobs ..... 2. *Neophyllophorus tritus* (Sluiter)

1 *Neophyllophorus destic*

FIG. 68: 14-16

Phyllophorus destichadus Deichmann, 1930, p. 146, pl. 18, fig. 3; 1938, p. 135, pl. 1, figs. 15–18; 1941, p. 135 (passim); H. L. Clark, 1933, p. 112.

Diagnosis.—Up to 6 to 7 cm. long, in preserved condition, with 15 to 20 tentacles, of different size, in two indistinctly separated circles. Color brownish purplish. Spicules tables with delicate, oval disk with four large, squarish holes and four smaller wedge-shaped ones; spire two-pillared, with 8 to 12 spines on top. Type: Museum of Comparative Zoology. Type locality: Tortugas. Distribution: Known from Tortugas and Biscayne Bay, Florida, collected at low tide. Both the Tortugas and Biscayne Bay specimens were collected by H. L. Clark who dug them out from eelgrass roots in firm mud.

A closely related form is known from the Panamic region (Deichmann, 1941).

2 *Neophyllophorus tritus* (Sluiter)

Thyone trita Sluiter, 1910, p. 339, text figs. E, a–e.
Phyllophorus tritus Deichmann, 1930, p. 147, pl. 18, figs. 4–8; H. L. Clark, 1933, p. 113.

Diagnosis.—Few cm. long in preserved condition; tentacles 18, probably 20 in mature specimens. Color grayish violet to deep purplish. Spicules tables with four large holes and four smaller ones in the oval to rectangular disk; spire with two pillars, sometimes reduced to knobs. Type: Possibly in Germany. Type locality: Bird Key Reef, Tortugas, Florida. Distribution: Taken at Tortugas, Florida, and Antigua, British West Indies. The small size may indicate that the species is based on immature individuals. It may be that it is the young of *destichadus* in which the spicules are less characteristic and for some reason have been partly resorbed, something I have never seen in typical specimens in which the edge of the tables always is firm and even.

Genus 4 LIPOTRAPEZA H. L. Clark, 1938

Genus established for *Phyllophorus vestitiens* Joshua, and two other Pacific forms; the latter have, however, proven to belong in other genera. For the present one West Indian species has been included.

Lipotrapeza seguroensis (Deichmann)

FIG. 68: 6-11

Phyllophorus seguroensis Deichmann, 1930, p. 141, pl. 17, figs. 10–13.
Euthyonidium seguroensis Deichmann, 1938e, p. 132, figs. 9–14 (with field note by H. L. Clark).

Diagnosis.—Small forms 5 to 6 cm. in preserved condition, with flexible, soft skin, though rough to the touch. Feet scattered over entire body; tentacles 20 in two circles with five large pairs and five small inner pairs. Color mottled brown. Calcareous ring short, tubular, with insignificant posterior prolongations. Spicules numerous regular tables with four central holes and about 12 marginal ones; margin undulated to blunt dentate. Spire with four pillars and a number of spines on the top. Feet with end plate but no supporting rods. Introvert with tables and rosettes; tentacles with small perforated rods and rosettes in the distal part. Type: Museum of Comparative Zoology. Type locality: Porto Seguro, Brazil. Distribution: Known from Brazil, Jamaica, and Tortugas and Cape Florida in Florida. Taken near low tide mark. Near Cape Florida H. L. Clark dug it out of sandy mud in grassy flats. It may very likely be found widespread in suitable localities in the southern part of the Gulf.

Genus 5 PHYLLOPHORUS Grube, 1840

Phyllophorus dobsoni Bell

Phyllophorus dobsoni Bell, 1883, p. 60, pl. 5, figs. 5, 5a–b; Deichmann, 1930, p. 141.

Diagnosis.—Type 8 cm. long, barrel-shaped, with conical feet scattered over the entire body. Color brownish. Calcareous ring short, tubular with short posterior tails. Spicules small disks, with four or more small holes and a few scattered knobs. Type: British Museum. Type locality: Bay of Honduras. So far no other specimens have ever been recorded, but one would naturally expect that the species would also occur in the Gulf of Mexico.

How the spicules are in young individuals is unknown, and the only other phyllophorid with similar spicules is Sluiter's *P. transveetus* from the East Indies known from the type and one other specimen. The similarity between the two species is so great that one wonders whether there possibly may be a mistake in the geographic location. Thus Domantay (1933) mentions a "Honduras Bay" in the Philippines, so there is the possibility that Bell's species might have come from that locality and not Central America.

Genus 6 BENTHOPHYLLOPHORUS nom. nov.

New name for *Thyonidium conchilegum* Pourtalès.

Benthophyllophorus conchilegum (Pourtalès), 1868

FIG. 68: 17–20

Thyonidium conchilcgum Pourtalès, 1868, p. 128; 1869, pp. 359, 361.

Phyllophorus conchilegum Deichmann, 1930, p. 142, pl. 17, figs. 14–15.

Diagnosis.—Small form, 4 to 5 cm. long, with 20 tentacles of unequal size in 2 indistinct circles. Feet few large, scattered. Skin stiff, rough from spicules. Color in alcohol whitish. Spicules tables with circular disk with about eight marginal holes, four pillars and spire ending in numerous small teeth. Introvert with large tables with irregular disk. Type: Museum of Comparative Zoology. Type locality: Off Sand Key. Distribution: Known only from the waters around Florida, from 100 to 189 fathoms depth. Lives undoubtedly in soft mud, judging from the content of the intestine. It is a typical deep water form with no affinities to any other known phyllophorid.

Order 4 MOLPADONIA

The West Atlantic members of this order were treated by Deichmann, 1940, and no changes have been made since that time.

KEY TO THE GENERA AND SPECIES OF MOLPADONIA KNOWN FROM THE GULF OF MEXICO

1. Thick-skinned forms with barrel-shaped body which tapers off into a long stout tail. Tentacles 15 with 2 pairs of lateral digits (and no terminal digit). Color dirty white. Spicules numerous, small disk-shaped bodies ("cross-cups"). Few fathoms depth ..... 2. *Paracaudina* Heding. One species. *Paracaudina obesacauda* (H. L. Clark), p. 406

1. Thin-skinned forms with barrel-shaped body which quickly contracts to a short thin tail. Tentacles 15 with a terminal digit and a few pairs of lateral digits. Spicules derived from tables or developed as huge rods or plates; in some species skin red from phosphatic bodies. 1. *Molpadia* Cuvier 2

2. Spicules chiefly one-pillared tables with three to six holes in disk; in older individuals fusiform rods or thromboid plates dominate. Usually numerous phosphatic bodies ..... 1. *Molpadia musculus* (Risso), p. 405

2. Spicules chiefly three-pillared tables 3

3. Tables large, with numerous holes; phosphatic bodies seem to be totally lacking ..... 2. *Molpadia barbouri* Deichmann, p. 406

3. Phosphatic bodies present in varying amount. Tables small with three to six holes in disk; numerous holes in disk of tables in tail ..... 3. *Molpadia cubana* Deichmann, p. 406

Genus 1 MOLPADIA Cuvier, 1817

1 *Molpadia musculus* (Risso)

See Clark, 1907, p. 165, pl. 23, figs. 4–7 (complete list of references); also Deichmann 1940, p. 225, pl. 40, figs. 1–15.

Diagnosis.—Large species up to 16 cm. long with varying amounts of phosphatic bodies. Spicules one-pillared tables with three to six holes often one to three marginal projections. In older individuals these spicules are superseded by huge fusiform rods or rhomboid plates. Tail with fusiform rods, with or without a small spire. Type: Lost. Type locality: Mediterranean Sea, undoubtedly from less than 200 fathoms. Distribu-

tion: Circumtropical, in some regions reaching Arctic or Antarctic waters. From less than 200 to more than 1,000 fathoms. The Museum of Comparative Zoology has one record from the Gulf of Mexico at about 28° latitude and 87° longitude, 1,560 fathoms depth, but all the *Atlantis* records are from outside the Gulf area so apparently the species is not common there.

2 *Molpadia cubana* Deichmann

FIG. 68: 21-22.

Trochostoma antarcticum Théel, 1886a, p. 16.
Nec T. antarcticum Théel, 1886a, p. 44, pl. 2, fig. 7.
Molpadia cubana Deichmann, 1940, p. 220, pl. 37. figs. 1–3.

Diagnosis.—Small species, less than 10 cm. long, with numerous phosphatic bodies and three-pillared tables with three large holes and a varying number of smaller holes. Tail with small tables with round to oblong disk with numerous holes. Type: Museum of Comparative Zoology. Type locality: Off Havana, 175-210 fathoms. Distribution: So far reported only from the waters around Cuba, off Yucatán and the coast of Texas. From about 200 fathoms (*Atlantis*); a single record from 1,440 fathoms may possibly be omitted as erroneous. Along the coast of Texas and on the shrimp grounds off Yucatán the species has been taken in less than 50 fathoms depth (13 to 37 fathoms, Hildebrand, letter).

3 *Molpadia barbouri* Deichmann

Molpadia barbouri Deichmann, 1940, p. 222, pl. 39, figs. 1–6.

Diagnosis.—Medium sized, 8 cm. long, with snow-white skin (in alcohol). Rigid from the numerous spicules which consist of three-pillared tables with disk varying from large with several circles of holes to smaller with few holes. Sometimes the spire is reduced so large plates result. Tail with small tables with elongate disk and minute spire. Type: Museum of Comparative Zoology. Type locality: Nicholas Channel, north of Cuba. Distribution: Waters around Cuba, from 390 to 605 fathoms.

The majority of the *Atlantis* records are definitely outside the Gulf region, but nevertheless, one may expect the species around the Yucatán peninsula.

Genus 2 PARACAUDINA Heding, 1931

Caudina (partim) *Auctores.*
Pseudocaudina Heding, 1931, p. 283 (preoccupied).
Paracaudina Heding, 1931, p. 455.

1 *Paracaudina obesacauda* (H. L. Clark)

Caudina obesacauda H. L. Clark, 1907, pp. 38, 176, pl. 9, figs. 1–5; Deichmann, 1930, p. 201, pl. 24, figs. 6–8.
Paracaudina obesacauda H. L. Clark, 1935, p. 284; 1940, p. 215.

Diagnosis.—Up to 15 cm. long with the barrel-shaped body gradually tapering off into the stout tail. Spicules in skin numerous cross-cups, mostly with bluntly rounded lateral projections, similar to those found in the New Zealand species, *P. coriacea*, and also common in the individuals of *P. chilensis* from off the tropical west coast of Central America and Mexico. Type: Museum of Comparative Zoology. Type locality: Marco, Florida. Distribution: Known from Key West and Tortugas, Florida, westward to Galveston, Texas. Few fathoms depth.

Usually large numbers are dredged from the same spot. More intensive collections will probably show that it is one of the most common forms in the Gulf in suitable localities. Its biology is completely unknown, but it will undoubtedly prove to be similar to that of the well studied Japanese form, usually called *P. ransonnetti* (v. Marenzeller) or *P. chilensis* (J. Müller).

Order 5 APODA Brandt, 1835

KEY TO THE FAMILIES KNOWN FROM THE GULF OF MEXICO

Spicules anchors and anchor plates; tentacles with slender digits ..... 1. *Synaptidae*, p. 406
Spicules wheels and sigmoid or bracket-shaped bodies; tentacles with broad stem with short, flat digits ..... 2. *Chiritotidae*, p. 408

Family 1 SYNAPTIDAE Oestergren, 1898

KEY TO THE GENERA AND SPECIES FOUND IN THE GULF OF MEXICO

1. Deep water form with large anchors with teeth on the arms; anchor plates with numerous dentate holes. Tentacles with one to two digits on each side. 4. *Protankyra* Oestergren ..... *Protankyra brychia* (Verrill), p. 408
1. Shallow water forms 2

2. Large species, up to 100 cm. long, with plume-like tentacles; reef dweller. 1. *Euapta* Oestergren.
Euapta lappa (J. Müller), p. 407
2. Small species, 10 cm. or less; tentacles with few digits. Lives in seaweed or burrows in sand or mud 3
3. No teeth on flukes; anchor plates with large central holes surrounded by six large holes, all dentate; complete transverse bridge. 2. *Synaptula* Oersted ..... *Synaptula hydriformis* (LeSueur), p. 407
3. A few teeth on flukes; anchor plates elongate, with large central holes, surrounded by six holes, more or less well equipped with teeth; incomplete transversal bridge. 3. *Leptosynapta* Verrill 4
4. Large anchors, 0.3 to 0.5 mm. long; miliary grains as C-shaped bodies, numerous everywhere
1. *Leptosynapta multigranula* H. L. Clark, p. 407
4. Small anchors, 0.2 mm. long or less; miliary grains not numerous, often in groups of three to five, developed as delicate curved rods with expanded or branching tips ..... 2. *Leptosynapta crassipatina* H. L. Clark, p. 407

Genus 1 EUAPTA Oestergren, 1898

1 *Euapta lappa* (J. Müller)

Synapta lappa J. Müller, 1850, p. 134.
Euapta lappa H. L. Clark, 1907, p. 73, pl. 4, figs. 23–25; Deichmann, 1930, p. 205.

Diagnosis.—Up to 100 cm. long, silvery gray, sometimes longitudinally striped. Stock of anchor branched or deeply cleft; vertex with minute knobs; anchor plates with distinct bridge. Type: Possibly in Germany. Type locality: "West India." Distribution: Widespread in the West Indies but not known from Bermuda. It is reported from the waters around Tortugas and may therefore be expected in Yucatán and along the north coast of Cuba. Théel lists it from Tenerife but that may be a case of erroneous labeling.

According to W. K. Fisher the animal is quite active, crawling around among coral rocks or on sand and to a limited extent able to swim (Deichmann, 1926, p. 27).

The species differ very little from the Indo-Pacific form, *E. godeffroy* (Semper). The latter is supposed to have the base of the digits of the tentacles united by a web, while the anchors often are deformed. Possibly a study of large series of spicules may show definite size differences.

Genus 2 SYNAPTULA Oersted, 1849

Synaptula hydriformis (LeSueur)

Holothuria hydriformis LeSueur, 1823, p. 162.
Synaptula hydriformis H. L. Clark, 1907, pp. 23, 82, pl. 6; Deichmann, 1930, p. 206.

Diagnosis.—Few cm. long, at utmost 10 cm. in life when expanded. Tentacles 10 to 15, with 5 digits on each side. Stock of anchors finely toothed; arms smooth, vertex with few knobs. Anchor plates with large central hole, surrounded by six large holes all more or less dentate; two large smooth holes at the posterior end and a distinct arched bridge across these holes. Miliary granules distributed in patches, visible with the naked eye. Viviparous; lives among algae. Type: Undoubtedly lost. Distribution: Common from Brazil to Bermuda, also around Tortugas and the southern Florida coast.

Two color phases exist, a brown and a green; the former is found among red or brown algae, the latter among green ones. Its life history has been worked out by H. L. Clark (1898) who found up to 179 young individuals escaping from a single female.

Genus 3 LEPTOSYNAPTA Verrill, 1867

1 *Leptosynapta multigranula* H. L. Clark

Leptosynapta multigranula H. L. Clark, 1924, p. 486, pl. 8, figs. 3–7; Deichmann, 1938, p. 135.
Leptosynapta multigranulata Deichmann, 1930, p. 207 (typographical error).

Diagnosis.—Up to 7.5 cm. in length in preserved condition. Tentacles 12, with 5 to 6 pairs of lateral digits, 2 to 9 sensory cups on the oral side of each tentacle. Spicules large anchors, 0.19 to 0.45 mm. long; anchor plates 0.2 to 0.29 mm. long. Miliary grains as C-shaped or ring-shaped bodies, scattered everywhere. Type: Museum of Comparative Zoology. Type locality: Tortugas, in sandy mud. Distribution: So far known only from Tortugas and Biscayne Bay.

The species seems to live in eelgrass covered flats and may very well have a much wider distribution than the present few records show.

2 *Leptosynapta crassipatina* H. L. Clark

Leptosynapta crassipatina H. L. Clark, 1924, p. 47, pl. 6, figs. 1–4; Deichmann, 1930, p. 208.

Diagnosis.—Few cm. long (types, 4 cm.) with 12 tentacles with 4 to 5 pairs of digits and 4 to 10 large sensory cups on the oral side of the tentacles. Spicules small anchors, 0.117 to 0.183 mm. long, with 3 to 7 teeth on each arm; anchor plates 0.11 to 0.14 mm. long. Miliary grains scarce, often in groups of 3 to 5, as delicate

curved rods with expanded or branching ends. Type: Museum of Comparative Zoology. Type locality: Near Key West, Florida. Distribution: From Key West northward and westward to Horn Island, Mississippi. The type specimens were dug out in a sandy mud flat in a mangrove key. The other specimens found in the Gulf have unfortunately all been preserved in formalin so the spicules are partly destroyed. A large series of this species and the foregoing is most desirable as they appear to me to be rather closely related and possibly represent different age stages.

Genus 4 PROTANKYRA Oestergren, 1898

Protankyra brychia (Verrill)

Synapta brychia Verrill, 1885, p. 539.

Protankyra brychia Oestergren, 1898, p. 116; Deichmann, 1940, p. 229, pl. 41, figs. 1–3.

Synapta abyssicola Théel, 1886, p. 14, pl. 1, fig. 11; Deichmann, 1930, p. 210.

Diagnosis.—Medium-sized form, 10 cm. long up to 1 cm. in diameter. Tentacles 12, with 2 pairs of digits. Color dark yellowish with reddish pigment on oral side of tentacle base. Spicules large anchors, 0.7 to 1.0 mm. long with branched handle. Anchor plates with numerous dentate holes and a bridge or an irregular network. No accessory miliary grains. Type: United States National Museum. Type locality: Off Cape Hatteras, at 938 fathoms. Distribution: Eastern and western Atlantic, including Gulf of Mexico. From 800 to 1,000 fathoms.

Usually, fragments are all that one gets of this mud-loving species. Although it is rather incompletely known it seems certain that the differences listed between Verrill's and Théel's species are within the limit of a variation which one must expect.

Lugwig's variety of *abyssicola* from the Pacific Ocean which H. L. Clark gave specific rank can undoubtedly be withdrawn as the presence or absence of teeth on the anchors is the result of age and not a constant character.

Family 2 CHIRIDOTIDAE

Genus 1 CHIRIDOTA Eschscholtz, 1829

Chiridota rotifera (Pourtalès)

Synapta rotifera Pourtalés, 1851, p. 15.

Chiridota rotifera, H. L. Clark, 1907, p. 115; Deichmann, 1930, p. 212; 1938, p. 136.

Diagnosis.—About 5 cm. long, occasionally 10 cm. with 12 (13–14) tentacles with 4 to 7 pairs of digits; numerous wheel papillae with wheels of varying size diameter, 0.1 to 0.2 mm.; curved rods thinly scattered. Viviparous. Type: Lost. Type locality: Biscayne Bay, Florida. Distribution: Known to range from Brazil, Trinidad to Bermuda, and also Tortugas, Florida.

According to Pourtalés it occurs "among interstices of the branches of a coral which occurs on shoals in Biscayne Bay," and from the findings in Bermuda and Tortugas, etc., one can expect it wherever broken corals and sand occur. Usually, many specimens are found in one spot, and as *S. hydriformis*, it is viviparous which Ludwig was the first to notice (1881), while H. L. Clark (1910) wrote an extensive report on its development.

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CHAPTER XIII

ANNELIDS AND MISCELLANEOUS WORMS

POLYCHAETOUS ANNELIDS OF THE GULF OF MEXICO

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For the purpose of this article the area of the Gulf of Mexico is limited to the approximately ellipse-shaped enclosure that terminates at its eastern end in Cape Sable, southern Florida, and at its other extremity in Cabo Catoche, northern Yucatán Province, Mexico. I exclude the northwestern end of Cuba and the Florida Keys, both of which fringe the Gulf of Mexico at the far eastern end, since in their polychaete fauna these areas may be regarded as part of the West Indian zoogeographic region and thus differ from that of most of the Gulf of Mexico.

The physical features of the area under consideration favor the development of an invertebrate fauna dominant in sand and mud dwelling species. Such are the habitats of many groups of marine annelids which may be expected to occur in prodigious numbers but which have still remained largely unknown. Based on records in the writer's possession, it can now be stated that there is a large endemic population; this may have had its origin within the enclosure of the Gulf and possibly in its center or western half. Thus, there are unique genera, a surprising number of undescribed species and subspecies. Some of them show marked affinities with the annelids of eastern United States, particularly in its southern end; others are akin with those of the Gulf of California and southern California. Still others have affinities with those of Brazil and less so with those of New England. Some species may be regarded as circummundane or be widely dispersed, thus common also to the Mediterranean Sea and western Europe. The annelids of western Florida are clearly related to those of the West Indies except for those species which may have been swept eastward from the western half of the Gulf. The floating logs, weeds, and other pelagic or drifting objects support an annelid fauna like that of the West Indies. The sponge, ascidian, and oyster-clump fauna appears to be similar throughout the Gulf.

The number of species which can be recorded from the literature is disappointingly small (less than 60). This number can be easily tripled when the records now in the writer's collections are published.[2] The records given below are based on species associated with a wide variety of habitats and only in a limited extent those from sand or mud flats. The last, however, should yield the richest fauna when the Gulf of Mexico will be more completely known.

The polychaetous annelids are summarized by family. The arabic number (1 to 59) preceding the name is consecutive. An asterisk preceding the name indicates that a change is newly made herein. The date following the original author's name is that of the erection of the species. The literature citations are listed at the end. A short appendix at the end summarizes ecological associations insofar as they are recorded.

Family POLYNOIDAE

*1. *Lepidametria commensalis* Webster, 1879.

As *Lepidasthenia lactea* Treadwell, 1939, pp. 3–4, figs. 13–15, from Galveston, Texas. Commensal in tubes of terebellid worms or free-living. Elsewhere known from eastern United States. The synonymy is here newly indicated.

*2. *Lepidonotus sublevis* Verrill, 1893.

As *Lepidonotus pallidus* Treadwell, 1939, p. 3, figs. 10–12, from Freeport, Texas, and as *Lepidonotus squamatus* Warren, 1942, p. 45, from Grand Isle, Louisiana. Occurs in crevices, in oyster clumps, in ascidian masses. Elsewhere known from eastern United States. The two synonymies are here newly indicated.

3. *Lepidonotus variabilis* Webster, 1879.

Reported by Warren, 1942, p. 45, from Grand Isle, Louisiana, and by Hartman, 1945, p. 10, from south-

[1] Contribution No. 120, from the Allan Hancock Foundation.

[2] See Hartman, O., 1951, The Littoral Marine Annelids of the Gulf of Mexico, in Pub. of the Institute of Marine Science 2 (1): 7–124, published since the preparation of this article.

western Florida. Occurs in crevices, under stones, in ascidian and sponge masses. Elsewhere known from eastern United States.

4. *Halosydna leucohyba* Schmarda, 1861.

Recorded by Rioja, 1946, p. 193, from Veracruz, Mexico, from between calcareous algae and mollusk shells. Elsewhere known from the West Indies and Bermuda.

5. *Harmothoë aculeata* Andrews, 1891.

Reported by Hartman, 1945, p. 10, from Lemon Bay southwestern Florida, under stones, in crevices, and on piles. Elsewhere known from North Carolina and Maryland.

6. *Harmothoë aculeata* (Treadwell), 1924.

Recorded by Rioja, 1946, p. 193, from Tecolutla, Mexico, from mollusk shells. Otherwise known from Barbados and Antigua, West Indies.

Family SIGALIONIDAE

*7. *Sthenelais ? articulata* Kinberg, 1855.

As *Eupholoe globosa* Winternitz, 1936, p. 3, figs. 6–12, from Apalachicola, Florida. This is here newly referred to the genus *Sthenelais* and questionably to the species *articulata* Kinberg. As the latter, it is known also from Brazil and the West Indies.

Family AMPHINOMIDAE

8. *Amphinome rostrata* (Pallas), 1766.

Reported by Augener, 1922, p. 39, from Veracruz, Mexico, and Campeche Bank, Gulf of Mexico, on floating logs. Widely recorded from Brazil northward through the West Indies and Gulf Stream to North Carolina.

*9. *Hipponoë multibranchiata* (Treadwell), new combination.

As *Metamphinome multibranchiata* Treadwell, 1940, pp. 1–2, figs. 1–3, from Galveston, Texas, on a floating log. This species is clearly separable from the nearly related *Hipponoë gaudichaudi* Audouin and Milne Edwards, known from the Gulf Stream, for having branchiae that are continued far back.

Family PHYLLODOCIDAE

10. *Eteone heteropoda* Hartman, 1951. Pub. Inst. Mar. Sci.

From Biloxi, Mississippi, sandy mud flats, also western and northwestern Florida and southeastern Texas, in sandy flats in littoral zones. Not taken outside of the Gulf.

11. *Nereiphylla fragilis* (Webster), 1879.

Recorded by Hartman (1951, Pub. Inst. Sci.), from Lemon Bay, Florida, and Port Aransas, Texas, from oyster and ascidian clumps. *Phyllodoce unicirrata* Winternitz, 1936, pp. 1–3, figs. 3–5, from Apalachicola, Florida, may be the same. Otherwise known from eastern United States.

12. *Eumida sanguinea* (Oersted), 1843.

Recorded by Hartman (1951, Pub. Inst. Sci.). Among shells, stones, in circummundane littoral zones.

Family PILARGIIDAE

13. *Ancistrosyllis bassi* Hartman, 1945.

Reported from Englewood, Florida, by Hartman, 1945, p. 15, and described by Hartman, 1947, pp. 501–504, pl. 61, from the Gulf of Mexico, North Carolina, and San Francisco Bay, California, in low or subintertidal sand flats.

14. *Loandalia americana* Hartman, 1947.

Described by Hartman, 1947, pp. 506–509, pl. 63, from Biloxi, Mississippi, Grand Isle, Louisiana, and elsewhere off San José Light, Guatemala, Pacific Ocean; in sand, littoral.

Family SYLLIDAE

15. *Autolytus brevicirrata* Winternitz, 1936.

Known only through the original description, Winternitz, 1936, p. 1, figs. 1–2, from Apalachicola, Florida. Incompletely characterized.

16. *Typosyllis corallicoides* Augener, 1922.

As *Syllis (Typosyllis) corallicoides* Augener, 1922, pp. 42–43, from Veracruz, Mexico, and not otherwise known.

Family NEREIDAE

17. *Neanthes succinea* (Frey and Leuckart), 1847.

Reported by Rioja, 1946, p. 194, and pp. 205–206, from Tecolutla and Veracruz, Mexico, from mangrove swamps associated with barnacles. Widely recorded from estuarine regions of temperate and subtropical regions of circummundane areas.

*18. *Nercis largoensis* Treadwell, 1931.

First described as *Nereis brevicirrata* Treadwell, 1929, pp. 3–4, figs. 1–4, from Key Largo, Florida (not *Nereis brevicirrata* Treadwell, 1920, pp. 467–468, figs. 1–4, from Santos, Brazil, which is, however, a species of *Perinereis*). This was later reported from Grand Isle, Louisiana, in sand, as *Nereis gracilicirrata* Warren, 1942, pp. 39–40, from a name taken from manuscript. The species is not known outside of the Gulf of Mexico and Florida Keys.

19. *Nereis pelagica occidentalis* Hartman, 1945.

First described from Beaufort, North Carolina, by Hartman, 1945, p. 20, pl. 4, figs. 1–6, and more widely recorded from the Gulf of Mexico from southwestern Florida to Louisiana, in sponge, oyster, and ascidian masses, from pilings, and from sandy shoals, in littoral zones. This may be the "Nereis pelagica" of Cary and Spaulding, 1909, p. 9, which comes from among oysters in Louisiana.

*20. *Nereis oligoholina* (Rioja), new combination.

Described as *Neanthes oligoholina* Rioja, 1946, pp. 207–210, pl. 1, figs. 4–6, pl. 2, figs. 13–19, from Tecolutla, Mexico, among roots of mangroves with barnacles. I refer the species to the genus *Nereis* since the notopodia have homogomph falcigers (Rioja, pl. 1, fig. 5). The species may be the same as *Nereis pelagica occidentalis*, above.

21. *Nereis riisei* Grube, 1856.

Recorded by Augener, 1922, p. 42, from Veracruz, Mexico, on corals and sponges. Elsewhere reported from both sides of subtropical and tropical America.

*22. *Laeonereis culveri* (Webster), 1879.

Reported as *Leptonereis nota* Treadwell, 1941, pp. 1, 3, figs. 7–10, from Offats Bayou, Galveston, Texas, presumably in muddy sand, and from southern Florida by Hartman, 1945, p. 21. The species is more widely known from North Carolina south to Brazil and the West Indies, in muddy sand. The synonymy is newly indicated herein.

23. *Lycastopsis tecolutlensis* Rioja, 1946.

By Rioja, 1946, pp. 211–212, pl. 1, figs. 7–12, from Tecolutla, Mexico, from mangrove swamps.

*24. *Platynereis dumerilii* (Audouin and Edwards), 1833.

Described as *Uncinereis trimaculosa* Treadwell, 1940, p. 3, figs. 4–9, from Galveston, Texas, on a floating log. It is known elsewhere from circummundane littoral regions. The synonymy is here newly indicated.

25. *Glycera americana* Leidy, 1855.

By Warren, 1942, pp. 42–43 from Grand Isle, Louisiana, and by Rioja, 1946, p. 194, from Tecolutla, Mexico, in tidal tributaries, in mixed sand. More widely recorded from east and west coasts of the Americas, and from South Pacific regions.

Family ONUPHIDAE

26. *Diopatra cuprea* (Bose), 1802.

By Cary and Spaulding, 1909, p. 9, from Louisiana, reporting tubes abundant on sandy shoals and sand flats, also by Warren, 1942, p. 44, from Grand Isle, Louisiana. The species is elsewhere known from tropical and subtropical eastern North and South America.

27. *Eunice schemacephala* Schmarda, 1861.

As *Leodice fucata* Warren, 1942, p. 45, from Grand Isle, Louisiana. This is the West Indian palolo worm, and more widely known in the Caribbean Sea.

28. *Marphysa sanguinea* (Montagu), 1815.

As *Marphysa aransensis* Treadwell, 1939, p. 5, figs. 16–17, from Aransas Pass, Texas, considered possibly the same as *M. sanguinea* in Hartman, 1944, p. 128. Occurs in hard packed mud or clay, in circummundane, warm-water regions.

29. *Palola siciliensis* (Grube), 1840.

Reported by Rioja, 1946, p. 194, from Veracruz, Mexico. Circummundane.

30. *Lysidice ninetta* Audouin and Edwards, 1833.

Reported by Rioja, 1946, p. 194, from Veracruz, Mexico, from among algae growing on tubes of *Sabellastarte*. Circummundane.

Family LUMBRINERIDAE

31. *Lumbrineris bassi* Hartman, 1944.

By Hartman, 1944, pp. 150–151, pl. 10, figs. 217–223, from Lemon Bay, Florida in sandy shoals. Not known elsewhere.

32. *Lumbrineris parvapedata* (Treadwell), 1901.

First described as *Lumbriconereis parva-pedata* Treadwell, 1901, p. 198, figs. 38–40, from Ensenada Honda, Culebra; later as *Lumbrinereis elongata* Treadwell, 1931, p. 3, fig. 2, from Grand Isle, Louisiana, and so reported by Warren, 1942, p. 45, from the same place; in sand. Not known elsewhere.

33. *Lumbrineris inflata* Moore, 1911.

By Hartman, 1944, p. 161, from the Gulf of Mexico, the Gulf of California, and the northeast Pacific Ocean; in sand.

Family LYSARETIDAE

34. *Lysarete brasiliensis* Kinberg, 1865.

As *Oenone brevimaxillata* Treadwell, 1931, pp. 1–3, figs. 4–9, from "Mexico," and tentatively relegated to *Lysarete brasiliensis* in Hartman, 1944, p. 185. Elsewhere known from the West Indies and eastern South America.

Family SPIONIDAE

35. *Nerine agilis* Verrill, 1873.

As *Nerine minuta* Treadwell, 1939, p. 5, figs. 18–20, from Port Aransas, Texas, in sand. The species is more widely known from eastern United States, and by Fauvel, 1950, p. 371, from French West Africa.

36. *Palydora websteri* Hartman, 1943.

As *Polydora ciliata* Kavanagh, 1940, pp. 31–34, and Kavanagh, 1941, p. 354, from Louisiana; also as *P. websteri* by S. Hopkins, 1947, bibliography, pp. 12–14, and Baughman, 1947, pp. 713–715. Penetrates commercial oyster shells and causes mud blisters. More widely known from eastern United States. The genus *Polydora* is reviewed by Stenzel and Turner, 1944, based on fossil records in eastern Texas.

Family CHAETOPTERIDAE

37. *Chaetopterus variopedatus* (Renier), 1847.

As *C. pergamentaceus* by Cary and Spaulding, 1909, p. 9, from Louisiana, on sand flats. Widely known from cosmopolitan areas in littoral zones.

Family ARENICOLIDAE

38. *Arenicola cristata* Stimpson, 1856.

By Warren, 1942, pp. 41–42, from Grand Isle, Louisiana, in sand. More extensively known from both sides of the Americas.

Family OPHELIIDAE

39. *Polyophthalmus pictus* (Dujardin), 1839.

By Rioja, 1946, p. 195, from Veracruz, Mexico, from encrusting algae. Considered cosmopolitan in distribution.

Family CAPITELLIDAE

*40. *Capitellides teres* Treadwell, 1939.

By Treadwell, 1939, p. 6, figs. 21–24, from Port Aransas, Texas. The single type specimen, examined by me, resembles a *Capitella*, but there are large genital hooks on the ninth setiger and large ova in the eleventh and twelfth segments, as in Capitellides. It departs from both these genera, however, in having setae, not hooks, in 8 anterior segments and in other respects. The species does not seem to fit any capitellid category (see Hartman, 1947, p. 400, for chart).

Family MALDANIDAE

41. *Branchioasychis americana* Hartman, 1945.

By Hartman, 1945, pp. 40–42, pl. 9, from Lemon Bay, southwestern Florida and more widely known from North Carolina. In fine sandy mud.

Family SABELLARIDAE

42. *Sabellaria floridensis* Hartman, 1944.

By Hartman, 1944, pp. 345–346, pl. 31, from southwestern Florida, and by Rioja, 1946, pp. 196–198, figs. 2–9, from Playa de Tecolutla, Mexico. Associated with shells. Not known elsewhere.

43. *Sabellaria vulgaris beaufortensis* Hartman, 1944.

Recorded by Rioja, 1946, pp. 195–196, fig. 1, from Tecolutla, Mexico, on mollusk shells, with the preceding species. This may be the *Sabellaria vulgaris* by Cary and Spaulding, 1909, p. 9, from Louisiana, on shells. Elsewhere known from North Carolina.

Family TEREBELLIDAE

44. *Pista cristata* (Müller), 1788.

Recorded by Rioja. 1946, p. 198, from Tecolutla, Mexico, on mollusk shells. Cosmopolitan in report.

45. *Loimia medusa* (Savigny), 1818.

Recorded by Hartman, 1945, p. 46, pl. 10, figs. 2, 3, from Lemon Bay, southwestern Florida, from large boulders in sand, below intertidal zones. Elsewhere known from all warm seas.

46. *Thelepus setosus* (Quatrefages), 1866.

Reported by Rioja, 1946, p. 198, from Veracruz, Mexico, in sandy tubes. Elsewhere known from cosmopolitan areas, in warm seas.

47. *Terebellides stroemi* Sars, 1835.

Recorded by Rioja, 1946, p. 198, from Veracruz, Mexico, in mud bottom from a few meters depth. Cosmopolitan in dredged depths.

Family SABELLIDAE

48. *Megalomma bioculatum* (Ehlers), 1887.

Recorded by Rioja, 1946, p. 199, from Veracruz, Mexico, from among algae. Elsewhere known from the West Indies.

49. *Hypsicomus circumspiciens* Ehlers, 1887.

By Rioja, 1946, p. 199, from Veracruz, Mexico, from mollusk shells. Common in West Indian seas and north of Venezuela.

50. *Sabellastarte magnifica* (Shaw), 1800.

By Augener, 1922, p. 48, from Veracruz, Mexico, and as *Sabellastarte indica* by Rioja, 1946, pp. 198–199, from Veracruz, Mexico. Reputedly circummundane in tropical seas.

51. *Branchiomma bairdi* (McIntosh), 1885.

As *Dasychone bairdi* Augener, 1922, p. 49, from Veracruz, Mexico. Elsewhere known from the West Indies and Bermuda.

Family SERPULIDAE

52. *Eupomatus protulicola* (Benedict), 1887.

Recorded by Rioja, 1946, pp. 199–200, figs. 10–13, from *Pinna* (mollusk) shells at Tecolutla, Mexico. More widely known from southeastern United States.

53. *Pomatoceros minutus* Rioja, 1941.

Reported by Rioja, 1946, pp. 201–202, from Veracruz, Mexico, on algae; elsewhere known from western Mexico.

54. *Pomatoceros* (*Pomatoleios*) *caerulescens* Augener, 1922.

By Augener, 1922, p. 50, from Campeche Bank, Gulf of Mexico. Not otherwise known.

55. *Eupomatus dianthoides* Augener, 1922.

As *Hydroides* (*Eupomatus*) *dianthoides* Augener, 1922, pp. 49–50, from Veracruz, Mexico. Not otherwise known.

56. *Vermiliopsis bermudensis* (Bush), 1907.

As *Vermilia bermudensis* by Rioja, 1946, pp. 200–201, from Tecolutla, Mexico, on mollusk shells. More extensively known from Bermuda.

57. *Vermiliopsis annulata* (Schmarda), 1861.

By Rioja, 1946, p. 201, from Tecolutla, Mexico, on mollusk shells. Otherwise known from the West Indies and Colombia on the Atlantic side.

58. *Salmacina dysteri* (Huxley), 1855.

By Rioja, 1946, p. 202, from Veracruz, Mexico, on tubes of *Sabellastarte*. Possibly circummundane in distribution.

59. *Mercierellopsis prietoi* Rioja, 1945.

Described by Rioja, 1945, pp. 412–417, 2 pls., from Tecolutla, Mexico and vicinity, in brackish water from mangrove esteros. Not otherwise known.

APPENDIX ON SOME ECOLOGICAL ASSOCIATIONS

Brackish or estuarine species:

Laeonereis culveri, Lycastopsis tecolutlensis, Neanthes succinea, Nereis pelagica occidentalis, Nereis oligohalina and *Mercierellopsis prietoi.*

Crevice dwellers, or on piles, or in oyster, ascidian, and sponge clumps:

Lepidonotus sublevis, Lepidonotus variabilis, Halosydna leucohyba, Harmothoë aculeata, Harmothoë trimaculata, Nereiphylla fragilis, Eumida sanguinea, Nereis riisei, Eunice spp.

Associated with algae:

Platynereis dumerilii, Lysidice ninetta, Eunice spp., *Polyophthalmus pictus, Megalomma bioculatum* and *Pomatoceros minutus.*

In sand or sandy mud or gravelly mud or mud and clay:

Sthenelais articulata, Eteone heteropoda, Ancistrosyllis bassi, Loandalia americana, Neanthes succinea, Nereis largoensis, Nereis pelagica occidentalis, Nereis oligohalina, Laconereis culveri, Lycastopsis tecolutlensis, Glycera americana, Diopatra cuprea, Marphysa sanguinea, Lumbrineris bassi, Lumbrineris parvapedata, Lumbrineris inflata, Nerine agilis, Arenicola cristata, Branchioasychis americana, Terebellides stroemi and *Mercierellopsis prietoi.*

On mollusk shells:

Sabellaria floridensis, Sabellaria vulgaris beaufortensis, Pista cristata, Hypsicomus circumspiciens, Eupomatus protulicola, Vermiliopsis bermudensis, Vermiliopsis annulota.

From floating logs:

Amphinome rostrata and *Hipponoë multibranchiata.*

Commensal in tubes of worms:

Lepidametria commensalis.

Boring in calcareous shells:

Polydora websteri.

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MISCELLANEOUS VERMES

By JOEL W. HEDGPETH, *Scripps Institution of Oceanography, University of California*

Phylum Echiurida

Information concerning this phylum in the Gulf of Mexico consists of two records for *Thalassema philostracum* Fisher (1947) which is known from the type locality, Thornton Island, near Englewood, Florida, and from a single specimen from Mustang Island, near Port Aransas, Texas, and a record of *Th. mellita* from Apalachicola Bay by Pearse and Wharton (1938). This latter record may actually refer to *Th. philostracum* which is also known from Beaufort, North Carolina. The Florida specimens were found in dead gastropod shells; the Texas specimen was found in a test of *Mellita quinquiesperforata*. The animal is rather small with a bright red body and a pale cream to white proboscis.

Phylum Sipunculida

Our knowledge of the Sipunculida of the Gulf of Mexico is based principally on collections in the vicinity of Key West and Tortugas, Florida. A total of 11 species is known to occur in the Gulf of Mexico, 10 of them from Key West or Tortugas. One of these is also recorded from Cedar Keys, and the eleventh has been collected from Caminada Bay near Grand Isle, Louisiana. The available published information on these sipunculids will be found in two papers: Gerould (1913) and Fisher (1947).

Examination of the known sipunculid fauna of the Gulf of Mexico reveals that two species, *Golfingia* (=*Phascolosoma*, vide infra) *cinerea* and *Siphonomecus multicincta* are so far known only from Key West, and one, *Golfingia cylindrata*, is known from Key West and Bermuda. The two species occurring in the more northern waters of the Gulf, *Phascolion strombi* (?) and *Dendrostoma alutaceum*, occur on the South Atlantic coast and are evidently eurythermal, especially the latter which occurs at Key West. The other species are widely distributed throughout the American tropical area. A curious anomaly is the absence of *Sipunculus nudus* from the northern Gulf coast in view of its wide distribution and occurrence at Key West. This may simply be an indication of inadequate collecting.

Genus GOLFINGIA Lankester

(*Phascolosoma* auct. nec Leuckart)

This best known of sipunculid genera is one of those victims of nomenclatural confusion which is a sadder aspect of taxonomic procedure. Fisher (1950) has reluctantly determined that the available name which must be used is Lankester's *Golfingia*, a name coined in commemoration of an excursion on the golf links with Professor MacIntosh at St. Andrews. Furthermore, *Phascolosoma* is actually the valid name for the species which have been hitherto included under *Physcosoma* by most recent authors.

Golfingia cylindrata (Keferstein).
Gerould, pp. 382–383, pl. 58, fig. 2.

A small (less than 1 inch long) species known from Key West and Bermuda.

Golfingia cinerea (Gerould).
Gerould, pp. 396–398, figs. 6–7.

Known only from a single specimen collected south of Key West in 45 fathoms.

Genus PHASCOLION Théel

Phascolion strombi (Montagu).
Gerould, pp. 403–416, figs. 9–11, pl. 60, figs. 10–13.

Specimens, apparently of this widely spread and variable species, have been found inhabiting shells of *Nassarius vibex* in Caminada Bay, Louisiana. They are small, and the identification is tentative.

Genus DENROSTOMA Grube

Dendrostoma alutaceum Grube.
Gerould, pp. 417–418, fig. 12, pl. 59, fig. 9.

This species is known from off Cape Hatteras, Key West, Tortugas, and Cedar Keys.

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Genus PHASCOLOSOMA Leuckart

(*Physcosoma* Selenka)

Phascolosoma varians Keferstein.
Gerould, pp. 419–420, pl. 62, fig. 18.

According to Gerould, this species is abundant in the Key West-Tortugas vicinity, and is also found on the southern coast of Florida. It occurs at Bermuda, Bahamas, and "among the West Indies," and at Ascension Island.

Phascolosoma antillarum Grube and Oersted.
Gerould, pp. 420–421, pl. 62, figs. 19–20.

Found at Key West in cavities in rocks, this species evidently occurs throughout the West Indian-Caribbean area, and has been taken on the Pacific side at Costa Rica, and on the coast of Chile.

Genus ASPIDOSIPHON Grube

Aspidosiphon speciosus Gerould.
Gerould, pp. 426–427, fig. 16, pl. 62, fig. 22.

Described from 3 specimens, 1 (the type) from Key West, another off Havana in 157 fathoms, and the third off the Brazilian coast at about 7° S in 20 fathoms.

Genus SIPUNCULUS Linnaeus

Sipunculus nudus Linnaeus.
Gerould, p. 428.

A widely distributed, cosmopolitan species, reported from Key West by Gerould (a single specimen).

Sipunculus polymyotus Fisher.
Fisher, pp. 354–358, fig. 54, pl. 10.

The species is based on two specimens from Key West. Another was collected off Long Bay, South Carolina.

Genus SIPHONOSOMA Spengel

Siphonosoma cumanense (Keferstein).
Gerould, pp. 432–435, pl. 60, fig. 14.

This species occurs in Oyster Bay, Florida, among oyster shells, and at Key West from sand along shore. It is also known from Venezuela and the West Indies.

Genus SIPHONOMECUS Fisher

Siphonomecus multicinctus Fisher.
Fisher, pp. 363–366, pl. 13.

Known from a single specimen collected at Key West.

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CHAPTER XIV

ARTHROPODS: XIPHOSURA, PYCNOGONIDA, AND CRUSTACEA

XIPHOSURA

By Joel W. Hedgpeth, *Scripps Institution of Oceanography, University of California*

The occurrence of *Limulus polyphemus* on the shores of the northern Gulf of Mexico is so limited that few biologists realize that it occurs there at all. To others, the statement of range given in such works as Ekman's Tiergeographie des Meeres, viz., New England to Yucatán, implies widespread occurrence in the Gulf of Mexico. Large populations of the horseshoe crab occur from Long Island to about St. Petersburg, Florida. Although *Limulus* is associated with bays and evidently requires estuarine conditions for optimum populations, its occurrence along the northern shores of the Gulf of Mexico is limited. It appears to be common only in the northeast corner. Cary (1906) reported an abundant population from the Chandeleur Islands, and it may be from this population that the sporadic records for Mississippi and Alabama result. According to records from the Alabama Museum of Natural History, *Limulus* was taken on Dauphin Island in August 1939, and several individuals, both males and females, were observed at night on April 20, 1948, in the same locality. A large male was taken at Wolf River, Baldwin County, on May 13, 1948. A specimen was collected from Santa Rosa Sound near Pensacola on February 20, 1938. The only trans-Mississippi record for this animal is of a specimen collected by C. T. Reed on Padre Island about 1940 or 1941. In view of the widespread occurrence of many invertebrates on both the Middle Atlantic and northern Gulf coasts this erratic distribution of *Limulus* is a curious anomaly. For a recent report on the natural history and breeding habits of *Limulus*, see Shuster (1950). In regions where the horseshoe crab is abundant, it may be a serious predator on soft clam beds, and control measures are being considered in Massachusetts. It is reassuring, however, to learn that control measures are considered costly and of doubtful efficacy as it would be a pity to exterminate one of our greatest zoological curiosities.

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PYCNOGONIDA

By Joel W. Hedgpeth, *Scripps Institution of Oceanography, University of California*

Our knowledge of the pycnogonid fauna of the Gulf of Mexico is restricted to a few dredge hauls in the northeast corner of the Gulf and some scattered hauls farther south, the shore and dredge collections at or near Tortugas, and a few shore and buoy collections on the Texas coast. Nevertheless, these records, particularly those from the Tortugas, are of considerable zoogeographical interest. Since the pycnogonids lack an active, free-swimming larval stage, they must rely upon passive means of dispersal. Several instances of pycnogonid larvae in medusae have been reported in the literature, and the occurrence of several species in the sargassum biota suggests an even more convenient vehicle for dispersal (see Hedgpeth, 1947, for discussion and summary of the literature). The distribution pattern of several species along the coasts of America, Europe, and Africa is similar to the occurrence of stranded leguminous seeds, the "sea beans," discussed with exhaustive thoroughness by Guppy (1917).

Another aspect of the fauna of special interest is the occurrence of a ten-legged species, *Pentacolossendeis reticulata*, along the southern edge of the Florida Keys. A cognate octopodous form, similar to the "normal" analogues of other ten-legged species, has not yet been found for *P. reticulata*. Its discovery would be a substantial buttress for the author's theory concerning the origin of ten-legged pycnogonids (1947), and further collections, especially along the 100-fathom line, should be of particular interest. The ten-legged *Pentapycnon geayi* Bouvier, known from French Guiana and north of Puerto Rico, can also be expected in Gulf waters, especially in the Tortugas area.

Aside from the congregation of small, inconspicuous species at Tortugas there are relatively few pycnogonids which are found in the waters of the Gulf of Mexico and which, on the basis of our inadequate information, might be considered characteristic of these waters. These have been indicated on a distribution map (fig. 69). The large prune purple pycnogonid, *Anoplodactylus lentus*, has been collected at several stations in the northeastern part of the Gulf, at Tortugas, and off Yucatán. A smaller form of this species is common along the Atlantic coast from Carolina to Woods Hole. Another species of this typically tropical, warm temperate genus, *A. insignis*, common at Tortugas, is found near Sanibel Island, in the northeast corner off Cedar Keys, and due west of Tortugas. It is common at Bermuda, and there is one record (the type locality) off Bahia, Brazil. Both of these species occur from near shore to moderate depths; *Anoplodactylus lentus*, to 150 fathoms; *A. insignis*, to 48 fathoms. Another large, conspicuous species, *Pallenopsis schmitti*, found in depths from 20 to 155 fathoms, occurs in the Tortugas area and off the coast of Florida near the Bahamas. This species has also been found north of Puerto Rico and the coast of Colombia. The only species of *Nymphon*, a predominantly cold-water genus known to occur in the Gulf, or the entire American tropical area, for that matter, is *Nymphon floridanum* known from Tortugas and off Cedar Keys.

The shore collections from the western Gulf are meager but interesting. *Anoplodactylus pygmaeus* has been found among the fouling growths on buoys near Galveston, and *Ammothella rugulosa* occurs among hydroids at Port Aransas. *Anoplodactylus pygmaeus* is found off the coast of Virginia, along the shore of southern England, and at Naples. *Ammothella rugulosa*, a small easily overlooked species, appears to be common at Tortugas and along the southern coast of Florida. It has been recorded from Brazil and Bermuda.

A conspicuous gap in the distribution of pycnogonids in the western Gulf of Mexico is the absence of *Endeis spinosa*, a situation confirmed by the extensive collections of organisms associated with fouling from New England to Panama

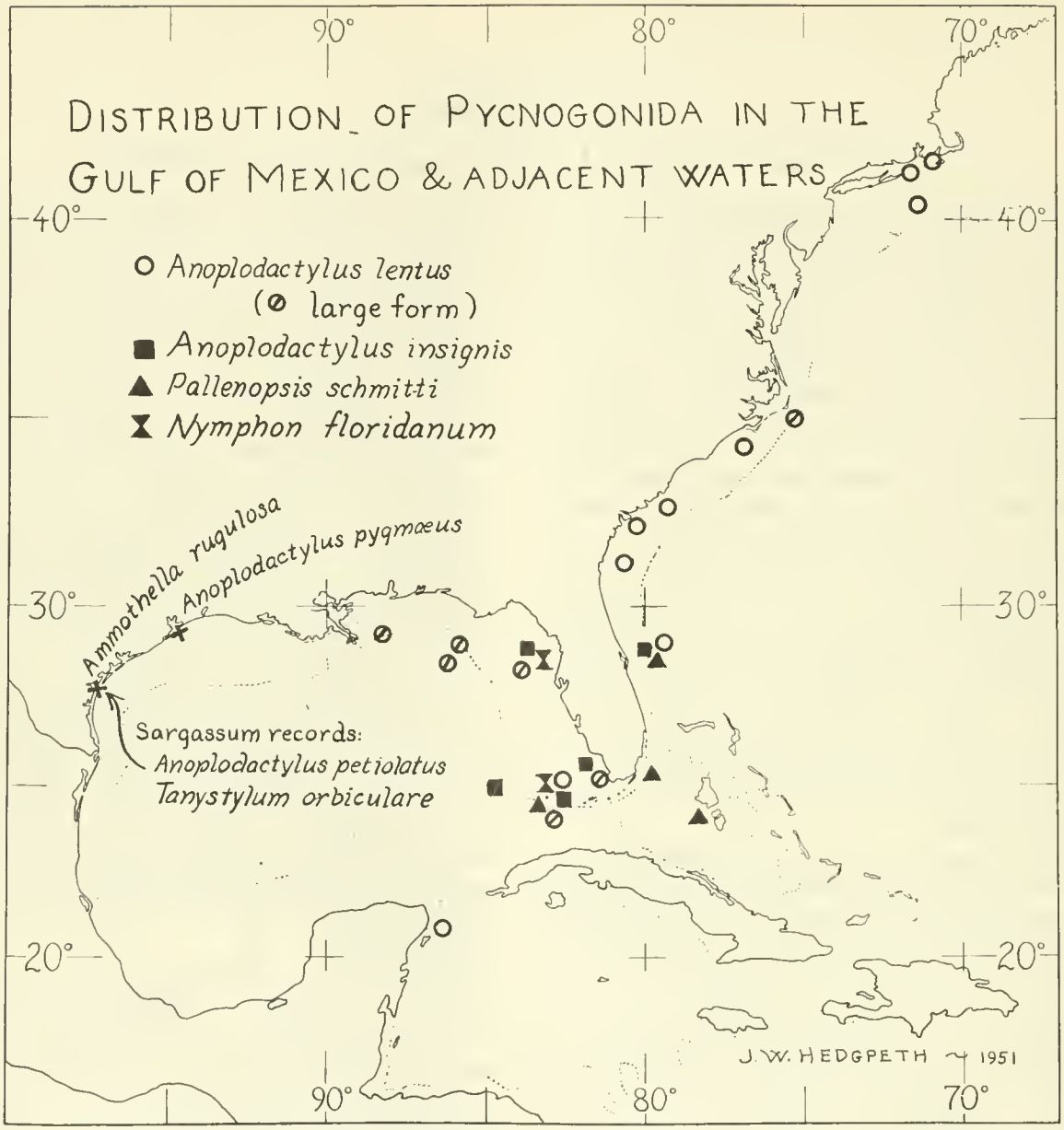

FIGURE 69.—Zoogeographical relationships of pycnogonids occurring in the Gulf of Mexico.

made by the Woods Hole Oceanographic Institution. Common at Tortugas, it occurs also on the shores of various Caribbean islands, the Bahamas, and Bermuda. It is one of the characteristic members of the sargassum fauna of the mid-Atlantic (Timmermann 1932) and occasionally occurs at Woods Hole. But, like the sargassum crab, *Planes minutus*, this pycnogonid has not been found on the sargassum which drifts ashore on the Texas and Louisiana coasts, and Tortugas is the only Gulf of Mexico record for both organisms. *Anoplodactylus petiolatus*, another species of the mid-Atlantic sargassum, has been collected from Texas sargassum. Another species, *Tanystylum orbiculare*, common at Woods Hole, has turned up on Texas sargassum and is the only sargassum record for this species. All other records for *T. orbiculare*, scattered along the Atlantic

coast between Georgia and Rhode Island, are shore or buoy collections. The species is also known from Brazil.

These distributional relationships are best summarized in tabular form. Descriptions and figures of all species included in this table will be found in Hedgpeth (1948). Some corrections in the troublesome genus *Callipallene* have been suggested by Stock (1952).

TABLE 1.—*Distribution of Pycnogonida occurring in the Gulf of Mexico*

Species	Gulf of Mexico	West Indies and Caribbean	Atlantic	Elsewhere	Depth (fathoms)
Nymphon floridanum Hedgpeth	Tortugas, northeast corner.				Surface—5.
Callipallene phantomo (Dohrn)	Tortugas		Norway-Azores	Naples, Black Sea.	
Callipallene brevirostris (Johnston)	Tampa, Fla		Norway; Portugal; Woods Hole; Virginia.		Shore.
Pallenopsis schmitti Hedgpeth	Tortugas	Puerto Rico, Bahamas, Colombia.	East coast, Florida		20–155.
Halosoma robustum (Dohrn)	do		Brazil	Mediterranean	Shore.
Anaplodactylus petiolatus (Krøyer)	Texas coast, sargassum.		Norway-France, Brazil	Naples	To 43.
Anoplodactylus pygmaeus (Hodge)	Texas coast, buoy fouling.		Norfolk, Va., England, Brazil.	do	Shallow water.
Anoplodactylus lentus Wilson	Tortugas, northeast corner.	Yucatán	Florida-Woods Hole		Shore—150.
Anoplodactylus insignis (Hoek)	Tortugas, Sanibel, northeast.		Bermuda, Brazil		3–48.
Anoplodactylus typhlops Sars	Tortugas		Norway, Ireland		To 582.
Anoplodactylus polignoci Bouvier	Sombrero Key		Cape Verde		Shore?.
Anoplodactylus evelinae Marcus	Tortugas		Brazil		Shore.
Anoplodactylus quadratispinosus Hedgpeth	Key West				?.
Anoplodactylus stylirostris Hedgpeth	Tortugas	Bahamas			Shore.
Anoplodactylus pectinus Hedgpeth	do				3–10.
Endeis spinosa (Montagu)	do	Hispaniola, Puerto Rico, Panama.	Florida-Woods Hole; Norway-France; Brazil.	Mediterranean, Black Sea.	Surface—38.
Achelia sawayai Marcus	do	Colombia, Venezuela	Brazil		Shore—25.
Achelia sp.[1]	Texas				
Ammothella rugulosa (Verrill)	Texas, Tortugas		Bermuda, Brazil		Shore.
Ammothella marcusi Hedgpeth	Tortugas				Do.
Nymphopsis duodorsospinosa Hilton	do		North Carolina (Folly River).	Galapagos, Baja Calif.	Shore—10.
Ascorhynchus latipes (Cole)	do	Hispaniola, Bahamas			Shore.
Ascorhynchus colei Hedgpeth	Florida Keys	do			Shore—80.
Eurycyde raphiaster Loman	Tortugas	Hispaniola, Bahamas, Colombia.		Cape Verde	Shore.
Tanystylum orbiculare Wilson	Texas (sargassum)		Virginia-Woods Hole, Brazil.		Shore—15.
Pentacolossendeis reticulata Hedgpeth	Florida Keys				98–100.
Pycnogonum reticulatum Hedgpeth	Tortugas, Key West			El Salvador	Shore.

[1] An immature form, taken with plankton net from the south jetty at Port Aransas, Tex. Cited here because it indicates the occurrence of this genus in the western Gulf.

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MARINE OSTRACODA

By Willis L. Tressler, *United States Navy Hydrographic Office*

The marine Ostracoda of the Gulf of Mexico region are very imperfectly known at the present time. George S. Brady, one of the earliest workers in this group to report ostracods from the Gulf region, published a series of papers from 1866 to 1887 and described a number of new species. Some of these descriptions were later incorporated into the report of the *Challenger* expedition, and many of them were published in the Marquis de Folin's work, Fonds de la Mer, which included four volumes published between 1867 and 1887. These volumes are very difficult to obtain, particularly the fourth volume which contains descriptions of several species of Ostracoda from the Gulf region. Unfortunately, almost all of Brady's descriptions are made from the valves alone, and for this reason many of his descriptions cannot be identified definitely with present day, living forms. Although his illustrations are beautifully executed, his descriptions are very brief and give little or no ecological data; not even the depth or exact location is given for most descriptions. Müller (1912), in his masterly compendium of the known species of Ostracoda, both marine and fresh-water, has allowed several of Brady's species, but for the most part his forms have been relegated to the doubtful species category or even to the "dubious genera and species" section of his book.

With the exception of Brady's work, only two other publications which deal with marine ostracods of the Gulf of Mexico are known despite the efforts of several geologists and zoologists who have been working on recent and fossil ostracods from this region. Dr. Henry V. Howe of Louisiana State University and his students, for example, have done considerable work on this group. The two publications referred to above both appeared in 1949 and consist of a preliminary report on ostracods obtained from bottom and core samples taken by the Woods Hole Oceanographic Institution research vessel *Atlantis* in 1947 by W. T. Rothwell, Jr. (1949), and a short report on some marine ostracods from Tortugas by the present author (Tressler 1949).

Rothwell's report was merely an abstract of his findings, but through the kindness of this worker, the present author was able to use his data sheets which give the location and depth of all species which he had taken from the bottom sediment samples. Rothwell distinguished 126 distinct forms but was not able to identify all of these to species. Some 40 of this number, which had been identified to species, were selected as being readily enough identifiable from the valves alone to leave no doubt as to their validity. Only five species were recovered with inner body parts intact, plus three other forms which were not definitely identified to species. The remainder of Rothwell's species were determined from the valves alone. Without these data this report would have been meager indeed. It is to be hoped that Dr. Rothwell will be able to complete his identifications, many of which will undoubtedly turn out to be new species, and publish a report on the complete collection at an early date.

The author has not been able to obtain a copy of Folin and Perier's Fonds de la Mer containing many of Brady's reports, but all species enumerated in volumes 1, 2, and 4 have been evaluated in Müller's (1912) comprehensive report. Also, it has not been possible to go through the paleontological literature which undoubtedly contains references to forms which are living today. One paper (Van den Bold, 1946) is cited in the literature as an example of such reports. Paleontological material is, of course, restricted by its very nature to identifications based upon shell structure alone. The short literature list also includes all other known reports on marine Ostracoda for the whole eastern Atlantic coast, because, while some forms are definitely restricted by temperature conditions, many, which are found at high latitudes, will also be found at

great depths in more southern waters, and for this reason some of the papers cited may be of use in identification of species in the Gulf region. The littoral and very shallow water ostracods of the Gulf of Mexico have scarcely been studied, but judging from the small amount of work which has been done on this ecological realm (Tressler 1940; Tressler and Smith, 1948), the so-called "barren zone" of Rothwell, lying between the strand and about 20 meters depth, should furnish many species.

ECOLOGY

With the limited data available little can be said of the ecological relationships of the species known from this region, and most of this is dependent upon Rothwell's information which he has kindly placed at the author's disposal.

Only 56 species of marine ostracods have been reported from the Gulf of Mexico proper and 19 additional species from the West Indies, Caribbean Sea, and adjacent areas. Most of these species have been reported from the northwest sector of the Gulf.

Rothwell divided the region of the Gulf in which he was working into five zones based upon depth and on the nature of the shelf area, as follows: (1) a Barren Zone between 10 and 24 meters depth, (2) the Marginal Shelf Zone between 24 and 68 meters, (3) the Upper Continental Slope between 68 and 190 meters, (4) the Lower Continental Slope between 190 and 1,250 meters, and (5) the Deep Sea Zone beyond 1,250 meters depth. If we examine the ostracods for which depth data are available, we find that 10 out of the 12 species reported from near Tortugas are in the "Barren Zone." This anomaly may be explained by the fact that Rothwell's samples were all taken with small-diameter punch coring devices or by small bottom samplers; sampling by means of a dredge over a greater area of the bottom would undoubtedly have recovered as many species of ostracods in the shallower water as were found in the beach samples at Beaufort (Tressler 1940) and in shallow water at Solomon's, Maryland (Tressler and Smith, 1948). The species found in the barren zone included *Cytherura lineata, Loxoconcha elegans, Cytherideis silicula* and *Paradoxstoma ensiforme* in the northwest sector and the following from Tortugas: *Cypridina squamosa, Asterope mariae, Asterope elliptica, Cyclasterope tripla, Cyclasterope sphaerica, Pontocypris intermedia, Macrocypris africana, Macrocypris schmitti, Nesidea cushmani, Xestoleberis punctata.*

No species was found exclusively in the Marginal Shelf Zone, but a number of forms were found only in this region and in the adjacent Upper Continental Slope down to 190 meters. These included *Paracytherois flexuosa, Cytherella polita, Macrocypris similis, Paradoxstoma ensiforme,* and *Cythereis silicula.*

Ostracoda which were found in the two preceding zones and in the Lower Continental Slope Zone as well as down to a depth of 1,250 meters included *Argilloecia cylindrica, Macrocypris decora, Cytherella obtusata,* and *Cythereis margaritifera.*

Five species were confined to the Lower Continental Slope and the Deep Sea Zones. These are *Nesidea victrix, Krithe tumida, Pontocypris trigonella, Xestoleberis expansa,* and *Cypridina flatus.* Four species were found only in the Deep Sea area: *Nesidea ovata, Bythocypris bosquetiana, Macrocypris tumida,* and *Pseudocythere caudata.*

The deepest station at which ostracods were collected was 3,630 meters located southeast of Brownsville; two species were found here, *Krithe tumida* and *Xestoleberis expansa.* Several species were, however, found at depths below 3,000 meters. These included, besides the two mentioned above, *Cythereis echinata* (3,157 meters), *Cythereis erica* (3,220 meters), *Cythereis stolonifera* (3,246 meters), *Cythereis dictyon* (3,475 meters), and *Cytheropteron mueronalatum* (3,431 meters).

With the exception of the genus *Conchoecia,* represented by one species, *C. atlantica* from Tortugas, and the males of the genus *Asterope* (*A. mariae* and *A. elliptica*) also from Tortugas, all the ostracods so far reported from the Gulf of Mexico are bottom-dwelling forms. *Conchoecia* is a true pelagic species and one of the very few found among the Ostracoda. The females of the genus *Asterope* keep close to the bottom, whereas the males are active swimmers and ascend to the surface where they are often taken in plankton catches. The nature of the bottom sediments on which the Ostracoda of the Gulf of Mexico are found varies considerably with the area, depth, and the species of ostracod, but unfortunately, for security reasons this subject cannot be discussed within the limits of this report.

Rothwell labels his barren zone as a region of lower salinity situated as it is along the coast where it receives inflow from several large rivers (Rio Grande, Brazos, Atchafalaya, and others). The species found within this zone are mainly forms whose close relatives have also been found in the brackish waters of the Solomons, Md., region at shallow depths.

Some ostracods are restricted by temperature in their world-wide distribution and are found only in northern latitudes or in deep water in other areas. *Bythocypris bosquetiana*, for example, although widely distributed, apparently prefers cold water. Other species, such as *Cythereis echinata*, appear to be widely tolerant of temperature variations and in the Gulf of Mexico, as in other localities, are found at all depths and temperatures. In the Gulf of Mexico Rothwell gives the limits of seasonal variation in bottom temperature as 75 meters which, in the region between Galveston, Tex., and Atchafalaya Bay, La., places its outer limits at the inner portion of the Upper Continental Slope. Beyond this depth bottom temperatures are cold the year round which accounts for the large number of species found beyond 75 meters as compared with the number found in the shallower areas where ostracods and other animals must have wide temperature tolerances.

The section following deals with the individual species which have been reported from the Gulf of Mexico up to the present time. Further details of taxonomy, structure, and individual habits may be obtained for many of these species by consulting references listed, particularly the monumental work of Georg Ossian Sars on the Crustacea of Norway, volume 9, Ostracoda (Sars 1928). Of all the references cited, this work should prove as helpful as any one report in identifying a large majority of the Gulf species. Müller's (1894) Ostracoda of the Gulf of Naples will also be found useful. Brady's papers, if used in connection with Müller's (1912) synopsis, will be of some help, particularly where one must depend upon identification from shells alone.

Suborder MYODOCOPA

Family CYPRIDINIDAE

Cypridina squamosa Müller, 1894

This large active swimmer lives on the bottom and has been reported only from the Tortugas Islands in the Gulf region. It was found at depths of from 20 to 22 meters. It is also known from the Gulf of Naples.

Cypridina flatus Tressler, 1949

A single female was taken at a depth of 1,200 meters near Tortugas. It has not been reported elsewhere in the world.

Asterope mariae (Baird, 1850)

Of all the known ostracods this genus alone possesses gills. Females usually stay close to the bottom; the males, however, may be taken in plankton tows close to the surface. Two females belonging to this species were found in shallow water near the Tortugas Islands. It is known from widely scattered places such as the coasts of Sweden, British Isles, France, Norway, the Mediterranean, North Atlantic, South Atlantic, Pacific, and off Vineyard Sound.

Asterope elliptica Philippi, 1840

This species is similar to *A. mariae* but has a shorter shell. Specimens have been reported from shallow water (4–5 meters) near Tortugas. Its distribution includes the Mediterranean and North Atlantic.

Cyclasterope priacanthus Tressler, 1949

The genus *Cyclasterope*, although closely related to *Asterope*, differs from it in having much higher shells some of which are almost spherical when seen from the side. *C. priacanthus* was reported from the stomach of the glass-eyed snapper, *Priacanthus cruentatus*, near Tortugas.

Cyclasterope sphaerica Tressler, 1949

In water 20 to 22 meters deep near Tortugas. Unknown elsewhere.

Cyclasterope tripla Tressler, 1949

Found in shallow water (on rocks at low tide and 18–20 meters) near Tortugas.

Family HALOCYPRIDAE

Conchoecia atlantica (Lubbock, 1856)

Members of the genus *Conchoecia* are true pelagic ostracods and although often found on the bottom, they are active swimmers. The genus is a large one of nearly 100 species and is widely distributed throughout most of the oceans of the world. One specimen of *C. atlantica* was taken

from the stomach of a fish caught at 160 to 200 meters depth near Tortugas.

Suborder CLADOCOPA

Family POLYCOPIDAE

Polycope orbicularis Sars, 1866

The genus *Polycope* is easily distinguished by the almost completely circular form of the shells which are smooth and glistening, without hairs. Shells of this species were taken in bottom samples at depths of between 128 and 1,867 meters in the northwest portion of the Gulf southeast of Atchafalaya Bay. The distribution of this species includes the coast of Norway, Franz Joseph Land, Cape of Good Hope, and the North Atlantic.

Suborder PLATYCOPA

Family CYTHERELLIDAE

Cytherella lata Brady, 1880

The internal anatomy of species belonging to this genus, which is the only genus in the suborder, is entirely unlike that of any other member of the Ostracoda group. Both pairs of antennae are powerfully developed and can be extended in front but are not used as swimming organs as in other Ostracoda. The posterior antennae are broad and flattened and resemble the appendages of Copepoda. The present species, *C. lata*, was reported from empty shells at depths ranging from 46 to 1,720 meters in various locations in the northwest region of the Gulf, from Brownsville to Atchafalaya Bay. It has also been reported from the West Indies, the Azores, the coast of Brazil, the Banda Sea, and Torres Straits in the East Indies.

Cytherella polita Brady, 1869

This species, first reported from Haiti and Cuba by Brady some 80 years ago, has been recently reported by Rothwell from several locations in the northwest part of the Gulf off Galveston and west of Atchafalaya Bay in comparatively shallow water (29–132 meters). The distribution of this ostracod includes the Arabian Sea, New Zealand, and the coast of South America near the Rio de la Plata.

Cytherella obtusata (Müller, 1912)

Shells of this species were reported in water at depths of from 43 to 198 meters off the coast of the northwest portion of the Gulf from Matagorda Bay to near Atchafalaya Bay. It was originally reported by Brady as *C. truncata* in the Caribbean off Colon (1869) and has since then been taken in Torres Straits.

Suborder PODOCOPA

Family CYPRIDAE

Pontocypris subreniformis Brady, 1880

Shells of this bottom form were taken in 1,600 meters off Brownsville and in 29 meters just west of Atchafalaya Bay. It has also been reported from the coasts of South Africa, Australia, Norway, and from the Arabian Sea.

Pontocypris trigonella Sars, 1866

Shells were found by Rothwell in samples taken at several places in the northwest sector of the Gulf at depths ranging from 190 to 1,417 meters. Its distribution includes the coasts of Norway, England, Haiti, Bermuda, and the Gulf of Guinea.

Pontocypris intermedia Brady, 1868

Five males belonging to this species were taken in an otter trawl in 20 to 22 meters of water off Tortugas. It has been reported from the Mediterranean as well.

Argilloecia cylindrica Sars, 1865

Specimens with internal body parts intact were taken by Rothwell at a depth of 44 meters off Brownsville, and shells were secured in the bottom samples at depths down to 823 meters in the sector of the Gulf between Brownsville and Galveston. This form is also well-known from the Norwegian coast, the North Atlantic, and the Mediterranean.

Macrocypris decora (Brady, 1865)

The large, usually whitish species of the genus *Macrocypris* are strictly bottom dwellers, being entirely devoid of swimming powers. While the actual shape of the shell varies with the species, they all have the characteristic elongated body with white glistening valves. *M. decora* was collected, with body structure intact, by Rothwell at a depth of 155 meters off Trinity Shoal west of Atchafalaya Bay. Shells of this species were taken at several places in the sector between Matagorda and Atchafalaya Bays at depths between 68 and 210 meters. This species appears

to be widely distributed throughout the Southern Hemisphere.

Macrocypris tumida **Brady, 1880**

Shells of this species were taken at between 1,400 and 1,800 meters depth nearly due east of Brownsville. The species is also known from somewhat shallower depths off the Kerguelens (50 meters), New Zealand (357 meters), and the southern coast of Norway.

Macrocypris maculata **(Brady, 1866)**

Shells of this ostracod were recovered from depths of between 57 and 1,720 meters at a number of stations in the northwest region of the Gulf. This species has been reported from the West Indies, the Caribbean, and Ceylon.

Macrocypris similis **Brady, 1880**

Shells were collected from bottom samples, at depths of 33 to 144 meters, taken off Galveston. Distribution includes the east coast of South America, Ascension Island (at a depth of 290–1,235 meters), and the coast of Ceylon.

Macrocypris africana **Müller, 1908**

Three females belonging to this species were collected in an otter trawl haul at depths of between 20 and 22 meters off the Tortugas. This ostracod was originally described from the coast of South Africa.

Macrocypris schmitti **Tressler, 1949**

Eight females were taken from cracked-up rock in shallow water on the west side of Loggerhead Key, Tortugas. This species is unknown except from this region.

Family NESIDEA

Bairdia coronata **Brady, 1870**

This doubtful form was described from specimens obtained off Veracruz in 1870 by G. S. Brady.

Nesidea ovata **(Bosquet, 1853)**

Shells of this bottom-dwelling ostracod were found in bottom samples taken in 1,810 meters of water a little north of due east from Brownsville. It has been reported from South Africa.

Nesidea victrix **(Brady, 1869)**

Shells of this species were collected at various stations in the northwest portion of the Gulf by Rothwell at depths ranging from 190 to 2,395 meters. It has been reported from the West Indies, the Caribbean (off Colon), the coast of north Brazil, and the west coast of North Africa.

Nesidea cushmani **Tressler, 1949**

Several females were collected at depths of from 4 to 22 meters off Tortugas. This is the sole record of this species at the present time.

Nesidea amygdaloides **(Brady, 1866)**

Brady reported this species from the Gulf of Mexico off Veracruz years ago. It is also known from the Australian coast, Cuba, Cocos Islands, New Caledonia, and the southern coast of Norway.

Bythocypris bosquetiana **(Brady, 1866)**

Species of this genus are bottom-dwelling. *B. bosquetiana* has been reported from the presence of shells at depths of 1,253 to 2,523 meters in the region east of Brownsville. Its distribution includes the West Indies, Atlantic Ocean, the Mediterranean, and Bass Straits (1,270 meters depth).

Bythocypris compressa **Brady, 1880**

Shells of this species were taken at depths varying from 66 to 1,920 meters at various locations in the northwest portion of the Gulf from Brownsville, the Sigsbee Deep, and as far as the mouth of the Mississippi River. This species had previously been reported from the South Pacific.

Family CYTHERIDAE

Bythocythere turgida **Sars, 1866**

Shells of this species, which is also bottom-dwelling, were obtained at depths of between 108 and 1,372 meters south of Atchafalaya Bay. It is known from the coast of Norway and the Gulf of Biscay.

Pseudocythere caudata **Sars, 1866**

This easily recognized and widely distributed ostracod was reported present (shells only) by Rothwell in samples taken at between 310 and 1,372 meters in the area south of Atchafalaya Bay. Its distribution includes the North Atlantic, Franz Joseph Land, coast of Norway, Mediterranean, the Kerguelens, and Prince Edward Island.

Cytherura lineata **Brady, 1867**

Numerous shells of this bottom-dwelling species were collected at various stations throughout the

northwest sector of the Gulf at depths ranging from 31 to 1,810 meters. This species had been reported only from the English coast previous to the present time.

***Cytheropteron alatum* Sars, 1866**

As their name implies, species of this genus have prominent wing-like lateral projections from the sides of the valves and are easily distinguishable for this reason. They are strictly bottom-dwelling forms. *C. alatum* shells were recovered from the bottom samples taken at depths between 31 and 1,920 meters at stations widely scattered throughout the whole northwest sector of the Gulf. Its known distribution includes the coast of England, Shetland Islands, the North Atlantic, coast of Norway, and at Funafuti.

***Cytheropteron mucronalatum* Brady, 1880**

Shells of this ostracod were collected in bottom samples at depths of between 174 and 3,431 meters at stations scattered over the northwest area of the Gulf. This species had previously been reported from the Pacific Ocean, between Japan and Patagonia, the Azores (2,515–3,748 meters), the North Atlantic, and between the Azores and the Bay of Biscay at 5,005 meters depth.

***Eucytherura complexa* (Brady, 1867)**

Shells were recovered throughout most of the northwest portion of the Gulf between Brownsville and the mouth of the Mississippi River at depths varying from 42 to 1,400 meters. This ostracod had previously been known only from the English and Norwegian coasts, and the Mediterranean.

***Paradoxstoma ensiforme* Brady, 1867**

These fragile-shelled forms, with their characteristic high posterior valve margins and suctorial mouths, are bottom-dwelling animals usually found near the coast in fairly shallow water. In the Gulf region, Rothwell reported finding their shells along the coast between the Brazos River and Atchafalaya Bay at depths of 16 to 90 meters. This species had been reported previously from the coasts of Norway and England, the Bay of Biscay, and the Mediterranean.

***Paracytherois flexuosa* (Brady, 1867)**

Although these ostracods somewhat resemble *Paradoxstoma* both in shape and in the presence of a suctorial mouth, *Paracytherois* may be distinguished from the other genus by the beak-like, rather than ring-formed shape of the mouth. Rothwell obtained specimens with body parts intact at 66 meters depth off Trinity Shoal near Atchafalaya Bay. Shells of this species were taken at a number of stations in the northwest sector at depths varying from 43 to 190 meters. *P. flexuosa* had previously been reported from the coast of Europe, the North Atlantic, and Franz Joseph Land.

***Xestoleberis minima* (Brady, 1866)**

Members of this genus, like some other groups of ostracods, have a brood pouch in the posterior part of the body for the reception of ripe ova for further development. The species *X. minima* was recorded by Rothwell from a specimen which he obtained with intact body parts at a depth of 88 meters off Galveston. Shells of this species were also found at various stations in the northwest sector of the Gulf at depths ranging from 68 to 210 meters. The species was earlier reported by Brady from shallow water in the West Indies.

***Xestoleberis expansa* Brady, 1880**

Shells were found at many stations in the northwest sector of the Gulf at depths of from 150 to 3,246 meters. This ostracod had been reported previously from off the Rio de la Plata at a depth of 3,473 meters and from the Arabian Sea.

***Xestoleberis curta* (Brady, 1866)**

Shells of this species were taken at depths of between 82 and 265 meters off the coast between Galveston and Atchafalaya Bay. It had been reported previously from many parts of the oceans in depths ranging up to 2,514 meters.

***Xestoleberis punctata* Tressler, 1949**

One female was collected in shallow water from the debris of cracked-up rock west of Loggerhead Key, Tortugas. It is unknown from other regions of the world at the present time.

***Loxoconcha avellana* (Brady, 1866)**

Species belonging to this genus are easily recognized by the short, rhomboid shape of the shell. *L. avellana* shells were found at stations throughout the northwest sector of the Gulf at depths of from 20 to 387 meters. Its known distribution includes the West Indies, Australia, Pacific, and Indian Oceans.

Loxoconcha elegans (Brady, 1870)

Shells of this ostracod were collected at several stations between Matagorda and Atchafalaya Bays in comparatively shallow water at depths of from 16 to 82 meters. It had previously been reported from Cuba and the Straits of Magellan.

Loxoconcha dorso-tuberculata (Brady, 1866)

This ostracod was found at only one station in the northwest sector of the Gulf in 190 meters off Atchafalaya Bay. It is known from the West Indies from which it was originally described by Brady years ago and from Noumea in the New Caledonia group of islands.

Eucythere declivis (Norman, 1865)

This genus contains forms which have a characteristically shaped shell, being much higher anteriorly than posteriorly. *E. declivis* shells were found in widely scattered locations in the northwest sector of the Gulf at depths of between 40 and 1,920 meters. Its distribution includes the coast of Europe, the North Atlantic, and Franz Joseph Land.

Krithe bartonensis (Jones, 1856)

The genus *Krithe* includes species with thin, smooth, and pellucid shells which have a broad marginal zone containing conspicuous pore canals. They are all bottom-dwelling and have poor powers of locomotion. *K. bartonensis* shells were found all over the northwest sector as far as the extent of the *Atlantis* cruises and in depths varying from 40 to 3,367 meters. It is a widely distributed form, being known from the European coast, Norway, Bay of Biscay, Iceland, North Atlantic, and Fiji Islands, at depths down to 3,200 meters.

Krithe tumida Brady, 1880

Shells of this species were collected at depths of from 197 to 3,630 meters in the northwest sector of the Gulf. This species had been reported previously from the North Atlantic, the region of the South Atlantic off the Rio de la Plata in 3,473 meters, and from Funafuti.

Cythereis dictyon Brady, 1880

Species belonging to this large genus all have rough, uneven shells which are often beautifully sculptured or covered with projections or spines. *C. dictyon* shells were found at many stations over the entire northwest sector of the Gulf at depths ranging from 63 to 3,475 meters. It is widely distributed throughout the oceans, being known from such regions as the Kerguelen Islands, Table Bay, Indian Ocean, and New Zealand. In general, it seems to be confined between north latitude 38° and 52° south latitude and has been found at all depths from 87 to 5,080 meters.

Cythereis echinata Sars, 1866

This easily recognized ostracod was reported from shells found at many localities in the northwest sector of the Gulf by Rothwell at depths of between 31 and 3,157 meters. It had been reported previously from the North Atlantic and the Norwegian coast.

Cythereis erica (Brady, 1880)

This species seems to be widely distributed over the northwest sector of the Gulf of Mexico at depths of from 25 to 3,230 meters. Its distribution includes the North Atlantic, the coast of Brazil (1,235 meters depth), and East Indies (915 meters depth), and off the Cape of Good Hope (2,624 meters).

Cythereis margaritifera Müller, 1894

Shells of this species were collected at three stations along the coast from Brownsville to Galveston at comparatively shallow depths which ranged from 29 to 265 meters. It was previously reported from the Gulf of Naples.

Cythereis pumicosa (Brady, 1870)

This species was reported from the waters off Veracruz by Brady. It has also been reported from Turk Island, New Providence, and Cuba in the West Indies.

Cythereis stolonifera (Brady, 1880)

Shells from this species were collected at a number of stations throughout the northwest sector at depths of between 88 and 3,246 meters. It is known elsewhere only from South Africa (Simons Bay).

Cythereis rastromarginata (Brady, 1880)

This ostracod appears to be widely distributed over the whole northwest sector of the Gulf and was reported from shells by Rothwell at depths of

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from 150 to 1,902 meters at widely scattered stations. The world-wide distribution includes the Pacific Ocean, Bass Straits, East Indies, Honolulu, and the Indian Ocean.

Cytherideis silicula (Brady, 1870)

The shells of this genus are long and comparatively very low in height. *C. silicula* was collected with body parts intact at depths of 31, 37, and 40 meters by Rothwell off Galveston, and shells of this species were taken along the coast from the Brazos River to Atchafalaya Bay in comparatively shallow water (18 to 174 meters depth). This species had previously been reported by Brady from off Veracruz.

Cytheridea setipunctata Brady, 1869

Brady reported this somewhat doubtful ostracod from the waters off Veracruz. This is the only known record of its distribution.

OSTRACODA REPORTED FROM ADJACENT REGIONS

A number of species of ostracods have been reported from areas immediately adjacent to the Gulf of Mexico. Although these species have not as yet been recorded from the Gulf proper, a list is included for future reference.

Caribbean Sea (Off Colon)

The following species have been reported by Brady for the Colon-Panama region of the Caribbean Sea and have been included by Müller (1912) in his compendium of the Ostracoda:

Paracypris pulchella (Brady, 1886).
Cythere compacta Brady, 1866.
Cythere oblonga Brady, 1866.
Cythereis speyere (Brady, 1868).
Cythereis rectangularis (Brady, 1869).
Cythereis ramdohri Müller, 1912.
Cythereis tuberculata (Sars, 1865).
Cytherella pulchra Brady, 1866.

West Indies

Müller records the following species from the West Indies:

Macrocypris tenuicauda Brady, 1870.
Nesidea subdeltoidea (Sars, 1887).
Nesidea longisetosa (Brady, 1902).
Bythocypris reniformis Brady, 1880.
Cythere duperrei Brady, 1869.
Cythereis tuberculata (Sars, 1865).
Cytheridea curta Brady, 1866.

Cuba

Two species have been described by Brady from the waters off the island of Cuba as follows:

Cythere compacta Brady, 1866.
Cytheridea subquadraregularis Brady, 1870.

Bahama Islands

Two species have also been reported from the Bahamas by Brady:

Xestoleberis angulata Brady, 1870.
Cythereis bahamensis (Brady, 1870).

Conclusions

It will be apparent from the above account that an almost unexplored field awaits the investigator in the taxonomy, ecology, and distribution of the marine Ostracoda of the Gulf of Mexico.

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COPEPODA

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In view of the admitted importance of copepods in the economy of the sea it is rather surprising that so little attention has been given the free-swimming forms of the Gulf of Mexico. This may, in great measure, be due to the fact that their systematic study entails much painstaking effort. They are small, and their precise determination requires microscopic dissection and the preparation of slide mounts. Also, the collecting of the specimens needed for an adequate review of the species and a knowledge of their distribution and the conditions of their existence in any large body of water is an expensive undertaking involving the employment of vessels, equipment, and men over a considerable period of time.

Not until the spectacular recurrence of the "red tide" in 1946–1947 had more than casual and localized samplings ever been attempted, but the comprehensive survey initiated at that time seems not as yet to have progressed beyond the list of species and a brief discussion published by King (1950). In his table of plankton distribution there are entered 67 copepods in 50 genera (excluding the pelagic stages of 2 parasitic forms belonging to 2 different genera). Thirteen of these were not accompanied by specific determination, so the number of species could easily be greater if any of these genera were represented by more than one species.

The earliest report enumerating Gulf species consists of Herrick's (1884) work in which he writes, "jottings . . . the result of a few days' stay on Mississippi Sound . . . will give some idea of the [copepod] fauna of the Gulf of Mexico." Of the eight free-swimming species he collected, two represented new species, one, indeed, a new genus. Along with their descriptions he published descriptive notes on five of the six other species.

Three years later Herrick's (1887) paper appeared in which the material on the species of the earlier report was reproduced with emendations and illustrations and two species added; two of the more or less tentatively identified forms of the earlier report were redescribed as new, of which one was referred to a different genus. The number of free-swimming salt and brackish water species recorded by Herrick from Mobile Bay and vicinity thus totals about 10. A few of these are again dealt with by Herrick and Turner (1895) but without particular reference to their occurrence in the salt or brackish waters of Alabama.

No further study of the free-swimming copepods seems to have been made until Foster (1904) prepared his notes on the free-swimming copepods of the waters in the vicinity of the Gulf Biological Station, Louisiana, in which 13 genera were presumably represented by 18 species, though at least 1 species in each of 6 genera was not specifically determined. Foster's specimens were collected 6 to 8 miles out in the Gulf of Mexico, in Calcasieu Pass, and in St. Johns Bayou which connects Lake Calcasieu with the Pass.

A representative of each of two genera not appearing either in King's table or in Foster's list were identified by Herrick also. With these exceptions King seems to have found about everything taken by those authors and, of course, many more genera and species besides. Otherwise, no extensive gatherings of free-swimming copepods have been reported on, though some very remarkable additions resulted from A. S. Pearse's visits to the former Tortugas Laboratory of the Carnegie Institution. In brackish ponds and pools Pearse (1932a) discovered four species of copepods in as many genera of which one genus and three of the species proved to be new records for the Gulf area. From among the numerous inhabitants of certain Tortugas sponges he (Pearse 1932b) sorted 23 different kinds of copepods not identified except as to the 12 genera to which the species belong. Nine of these likewise constituted new records. Finally, in the gill chambers of three species of crabs that he (Pearse

1932c) was examining for parasites he observed three species of free-swimming copepods, one species to a "host." These cannot be regarded as other than accidental guests. Again, two of the genera and perhaps all three species were first records for the Gulf.

Other than King's (1950) very recent preliminary report, little seems to have been done on the free-swimming forms since publication of Pearse's papers. Marsh (1910) remarks that Foster told him he had collected *C. aequoreus* in Lake Pontchartrain and connecting waters and adds, "It seems likely that further collections in brackish waters will show that this is not an uncommon form." Foster seems not to have recorded his observation in print. Davis (1948) netted a marine, a brackish water, and a more or less fresh water type of copepod in Long Lake, Dade County, which is connected with Garfield Bight, a shallow arm of Florida Bay, by a narrow and devious passage 4 miles long. The waters of the lake are distinctly brackish and even in periods of greatest rainfall are believed never to become completely fresh. The brackish water species, *Pseudodiaptomus coronatus*, had earlier been reported by Wright (1936) from the mouth of the Mississippi (Grand Pass and Point Chicot) from which the following year he described *P. americanus*. Mississippi Sound to the eastward is the type locality for Herrick's (1884, 1887, 1895) *P. pelagicus* which, because of its inadequate description, is conceivably identical with *P. coronatus* according to Wright (1937). The marine species proved to be new, while the fresh water form, if it is correctly one, was described as a variety of *Cyclops panamensis*. A newly described species, *Corycaeus americanus*, was added to the fauna by M. Wilson (1949) in part on the basis of material secured in a haul made off [Port] Aransas, Texas. Although the former United States Bureau of Fisheries steamer *Albatross* made one tow net haul in the Gulf of Mexico in 1885, the fact that it added 5 genera, 11 species of marine copepods to the list of those occurring in that body of water did not become known until C. Wilson (1950) reported on the *Albatross* collections.

Summarizing the foregoing information, one can safely say that close to a hundred free-swimming copepods, representative of some 70 genera, have to date been taken in the Gulf of Mexico and in brackish waters adjacent thereto. These, however, are believed to be but a small fraction of the species that an intensive Gulf-wide investigation would reveal.

Though less important economically parasitic copepods from the Gulf of Mexico came to the attention of naturalists at a much earlier date than the free-swimming forms, no doubt because of their association primarily with fish, their generally larger size, and the ease with which they can be collected. Perhaps the first to be recorded from the area was *Argulus funduli* described by Krøyer (1863) from New Orleans and recorded again by Bere (1936) from Lemon Bay, west coast of Florida, and Meehean (1940) from near New Orleans and from a brackish pool at Meveitta, Florida. For the greater part the species parasitizing Gulf fishes have been described principally by Bere and Meehean, just referred to, and, above all, by C. B. Wilson in a series of papers from 1902 through 1944. In all, just about 122 species have been reported from the Gulf after making allowance for duplications: Bere, 70 species; Meehean, 3 or 4 (without salinity readings, it is not always possible to determine whether the water in many localities in Florida may be wholly fresh or brackish); and C. B. Wilson, 48 (mostly in his Tortugas paper of 1935). Though not yet found on fish caught in the Gulf of Mexico, the 25 species of parasitic copepods which Wilson (1913) listed for Jamaican fish, not yet reported from the Gulf, will probably be found to occur there because the host species are common to both areas.

Of equal scientific interest are the parasitic copepods which infest the gills of Crustacea and, in one instance (*Pestifer agilis* Wilson, 1949), were found attached to the skin of an undetermined marine annelid dredged in 380 fathoms south of the Dry Tortugas. There are three species of these parasites of decapod Crustacea in the Gulf of Mexico: *Cancrincola jamaicensis*, originally described from the white land crab in Jamaica (Wilson 1913) and found later at Tortugas in the spider crab, *Microphrys bicornutus*, and the hermit, *Paguristes puncticeps* (Pearse 1932a; Wilson 1935); *Cancrincola plumipes* Humes (1941) described from adult marsh crabs, *Sesarma reticulatum*, at Grand Isle, Louisiana; and *Clausidium tenax* Humes (1949), also from Grand Isle from the mud shrimp, *Callianassa islagrande*.

This brief résumé of the work that has been done in striving for a better understanding and a

more thorough knowledge of the copepod fauna of the Gulf of Mexico, its relation to the other marine life of the area and its physical environment, shows that no more than a beginning has been made so far. Nevertheless, it is an encouraging beginning in view of the potentialities of the problem that it reveals. There is a considerable wealth of Gulf copepod material lying fallow in the collections of the U. S. National Museum that deserves attention in the light of the growing importance of the Gulf fishery resources now being actively developed by the current investigations of the Fish and Wildlife Service.

In Washington there are stored, as yet unstudied but still in good condition, considerable plankton collections made by the former United States Fish Commission and the Bureau of Fisheries steamer *Fish Hawk* in the Gulf of Mexico from as early as 1895 through 1901, 1902, 1903, 1912, 1913, and in 1914 as far to the westward as Lavaca Bay, Texas. These samples should have early attention, a small staff assembled to properly deal with them, and the necessary equipment provided. The U. S. National Museum provides unexcelled facilities for accomplishing these and similar tasks which will inevitably arise as the Gulf is more intensively studied. The student of copepods may have access here to the incomparable copepod library of the late C. B. Wilson that he bequeathed the Smithsonian Institution and to the extensive, authoritatively identified collection of specimens to which he devoted his life and upon which were based his many valuable publications dealing with the free-swimming and parasitic marine copepods of the world.

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CIRRIPEDIA: THE BARNACLES OF THE GULF OF MEXICO

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The following résumé of what is known about the barnacles of the Gulf of Mexico is based on (a) published accounts, the most important of which are the taxonomic studies of Pilsbry (1907, 1916) and the ecological studies of Stephenson and Stephenson (1950), and (b) unpublished data.[1] Pilsbry's material consisted of *Albatross* hauls and isolated shore collections, mainly from the western shores of Florida. Stephenson and Stephenson (1950) studied the Florida Keys area, and several authors have reported barnacles from several localities in the southern part of the Gulf. The unpublished data are based, primarily, on isolated shore collections in which the barnacles of Texas are especially well represented.

Until there is further study of the barnacles of this region, it is possible to draw no more than tentative conclusions concerning their horizontal and vertical distribution, the ecology, and the relationship to the fauna of adjacent areas.

The barnacles of the Gulf may be divided according to habitat into the littoral, the pelagic, and the deep water. Barnacles are probably not an important part of the intertidal fauna on most of the Gulf coast as rocky shores are very scarce, except in southern Florida. Wharfs, piles, and sea walls provide, however, a suitable substratum for several species. These barnacles, as well as some that are found in off-shore waters, also foul ships' bottoms in other parts of their range, and some, at least, may have been introduced into the Gulf in this way. Conditions in the Gulf appear to be much more favorable for the growth of pelagic and deep water barnacles.

A check list of the barnacles known to occur in this region follows (tables 1 and 2). For the sake of brevity, the region has been divided arbitrarily into six coastal areas, i. e., the Dry Tortugas, Florida Keys, west Florida, Mississippi, Louisiana, and Texas, and the deep water of the Gulf of Mexico.

[1] The author is indebted to Dr. Joel Hedgpeth for the opportunity of examining his barnacle collection, as well as that of the Texas Fish and Game Commission, and to Dr. Fenner A. Chace for the chance to study some of the Gulf barnacles acquired by the U. S. National Museum since Pilsbry's monographs were published.

TABLE 1.—*Check list of sessile barnacles in the Gulf of Mexico*

Species	Area	Number of localities	Reported by—[1]
Acasta:			
cyathus Darwin	Dry Tortugas	1	Pilsbry, 1916.
Balanus:			
amphitrite niveus Darwin	Florida Keys	1	Stephenson, T. A. and A., 1950.
Do	West Florida	6	Pilsbry, 1916.
Do	do	1	Kolosováry, 1943.
Do	do	2	Henry.
Do	Texas	1	Do.
amphitrite pallidus Darwin	Louisiana	1	Do.
calidus Pilsbry	West Florida	4	Pilsbry, 1916.
Do	Texas	1	Henry.
? *crenatus* Bruguière	West Florida	1	Kolosováry, 1943.
declivis Darwin	Dry Tortugas	1	Pearse, 1932b.
Do	West Florida	1	Pilsbry, 1916.
eburneus Gould	Florida Keys	1	Stephenson, T. A. and A., 1950.
Do	West Florida	1	Pilsbry, 1916.
Do	Mississippi	1	Do.
Do	do	1	Henry.
Do	Louisiana	3	Do.
Do	Texas	10	Do.
galeatus (Linnaeus)	West Florida	1	Pilsbry, 1916.
Do	do	1	Kolosováry, 1943.
Do	Texas	1	Henry.
improvisus Darwin	West Florida	1	Kolosováry, 1943.
Do	Mississippi	2	Henry.
Do	Texas	3	Do.
stultus Darwin	Dry Tortugas	1	Nilsson-Cantell, 1929.
triganus Darwin	Gulf of Mexico	1	Henry.

[1] Author's unpublished records are indicated by her name not followed by year.

TABLE 1.—*Check list of sessile barnacles in the Gulf of Mexico*—Continued

Species	Area	Number of localities	Reported by—[1]
Chelonobia:			
manati lobatibasis Pilsbry	West Florida	1	Pilsbry, 1916.
patula (Ranzani)	do	1	Do.
Do	do	1	Henry.
Do	Louisiana	1	Do.
Do	Texas	2	Pilsbry, 1916.
Do	do	1	Do.
testudinaria (Linnaeus)	Florida Keys	1	Henry.
Do	West Florida	2	Pilsbry, 1916.
Do	Texas	4	Henry.
Chthamalus:			
fragilis Darwin	Florida Keys	1	Stephenson, T. A. and A., 1950.
Do	West Florida	1	Pilsbry, 1916.
Do	Texas	2	Henry.
stellatus angustitergum Pilsbry	Florida Keys	1	Pilsbry, 1916.
Do	do	(2)	Stephenson, T. A. and A., 1950.
Platylepas:			
hexastylos (O. Fabricus)	West Florida	1	Pilsbry, 1916.
Do	Texas	1	Henry.
hexastylos ichthyophila Pilsbry	W. Florida	1	Pilsbry, 1916.
Pyrgoma:			
floridanum Pilsbry	do	1	Do.
Stomatolepas:			
praegustator Pilsbry	Dry Tortugas	1	Do.
Tetraclita:			
squamosa stalactifera (Lamarck)	Florida Keys	1	Do.
Do	do	(2)	Stephenson, T. A. and A., 1950.
Verruca:			
albo Pilsbry	Gulf of Mexico	1	Pilsbry, 1916.
floridana Pilsbry	do	1	Do.

[1] Author's unpublished records are indicated by her name not followed by year.
[2] Several.

TABLE 2.—*Check list of pedunculate barnacles in the Gulf of Mexico*

Species	Area	Number of localities	Reported by—[1]
Lepas:			
anatifera Linnaeus	Florida Keys	1	Pilsbry, 1907.
Do	Mississippi	2	Henry.
Do	Louisiana	1	Pilsbry, 1907.
Do	Texas	1	Henry.
anserifera Linnaeus	Florida Keys	1	Pilsbry, 1907.
Do	Mississippi	2	Henry.
Do	Louisiana	1	Pilsbry, 1907.
Do	Texas	1	Henry.
pectinata Spengler	Florida Keys	1	Pilsbry, 1907.
Do	Texas	1	Henry.
Octolasmis:			
forresti Stebbing	Dry Tortugas	1	Do.
Do	Florida Keys	1	Pilsbry, 1907.
Do	do	1	Henry.
Do	Texas	1	Do.
geryonophila Pilsbry	Dry Tortugas	1	Pearse, 1932a.
hoeki Stebbing	do	1	Henry.
Do	Florida Keys	1	Do.
Do	Texas	1	Do.
lowei Darwin	Dry Tortugas	1	Pearse, 1932a.
Do	W. Florida	1	Henry.
Do	Mississippi	2	Do.
Do	Louisiana	1	Pilsbry, 1907.
Do	do	1	Humes, 1941.
Do	do	1	Henry.
Do	Texas	2	Do.
Poecilasma:			
inaequilaterale Pilsbry	Florida Keys	1	Pilsbry, 1907.
inaequilaterale breve Pilsbry	Gulf of Mexico	1	Do.
kaempferi litum Pilsbry	Florida Keys	1	Do.
Scalpellum:			
antillarum Pilsbry	Gulf of Mexico	1	Do.
arietinum Pilsbry	do	1	Do.
diceratum Pilsbry	do	1	Do.
gibbum Pilsbry	do	1	Do.
portoricanum intonsum Pilsbry	do	1	Do.
regina Pilsbry	do	1	Do.
Do	do	3	Henry.
semisculptum Pilsbry	do	1	Pilsbry, 1907.

[1] Author's unpublished records are indicated by her name not followed by year.

The littoral barnacles with the widest distribution in the Gulf are *Balanus eburneus*, *B. amphitrite niveus*, and *Chthamalus fragilis*. In the Florida Keys the common intertidal barnacles of the rocky shore are *Chthamalus stellatus angustitergum* and *Tetraclita squamosa stalactifera*, with the *Chthamalus* occurring at the highest level of the midlittoral zone and the *Tetraclita* at a slightly lower level but overlapping the *Chthamalus* (Stephenson and Stephenson, 1950). The distribution of these two species in the Florida Keys is peculiar; both varied from absent to abundant on the oceanic sides of the keys and from absent to fairly common on the Florida Bay side, and no north-to-south effect could be demonstrated. *T. s. stalactifera* and *C. s. angustitergum* have not been reported from western Florida, although they might be expected to occur in the southern part.

B. eburneus and *B. a. niveus* range from the Florida Keys, where Stephenson and Stephenson (1950) found them commonly on walls, wharfs, and piles but never on the rocky platforms, to the Texas shore. The vertical range for both species is from a little above the low tide line to, at least, 25 fathoms. They are found oftener on wood or shells than on rock, and both are able to live in brackish water.

Chthamalus fragilis also ranges from the Florida Keys, where it is apparently rare, to the Texas shore. It is probably commoner on the northern shores of the Gulf than is indicated by the records, as members of this genus are often overlooked by collectors because of the small size and inconspicuous form. The vertical distribution is unknown for the Gulf, but it occupies a high level of the intertidal zone in other parts of its range.

Below low tide line the most widespread barnacles are *B. galeatus*, situated on gorgonians, and *B. calidus* on shells of all kinds and on dead echinoderms. According to Hedgpeth (personal communications), *B. galeatus* is commonly found on stems of gorgonians which have drifted onto the Texas beach.

The other species of *Balanus* occurring in the littoral zone have been found at only one or two localities so one can only guess at their distribution. *B. improvisus* will probably be found along the northern part of the Gulf, wherever a suitable substratum (wood, shells, and rock) is found, as this species, like *B. eburneus* and *B. a. niveus*, is partial to brackish water. In other areas the vertical distribution of this species is from the low tide line to 150 meters. *B. trigonus*, in other parts of its wide range, occurs from 1 to 3,000 meters on shells, crabs, and sponges. These two species, as well as *B. eburneus* and *B. a. niveus*, are important fouling organisms in other areas, but what part they play in the fouling of ships in the Gulf is unknown.

The barnacles, *B. declivis*, *B. stultus*, and *Acasta cyathus*, which live in sponges have been reported from the southern part of the Gulf, but an examination of the sponges of other parts of the Gulf will no doubt extend the distribution.

In addition to the barnacle-gorgonian and barnacle-sponge associations mentioned above, three other barnacle-associations occur in the Gulf. The barnacle-coral association is practically unknown, as apparently coral has not been examined for barnacles. One species of *Pyrgoma* has been reported by Pilsbry (1931) in coral. Of the turtle barnacles, *Chelonobia testudinaria* is widely distributed in the Gulf as is probably *Platylepas hexastylos* (a subspecies has been found on a fish in western Florida by Pilsbry, 1916). A subspecies of *C. manati* and *Stomatolepas praegustator* are known from only one locality in the Gulf.

The barnacles associated with crabs of the Gulf may be externally on the carapace and internally on the branchiae. *Chelonobia patula* and three species of *Poecilasma*, both of which are mainly on crabs, in addition to four species of *Balanus* (*a. niveus*, *improvisus*, *eburneus*, and *trigonus*) may be found on the carapace. Three species of *Octolasmis* occur on the branchiae. The shallow water crab, *Callinectes sapidus*, is the host of at least the first three species of *Balanus* enumerated above, *C. patula*, *Octolasmis lowei*, *B. trigonus*, *Poecilasma*, and all three species of *Octolasmis* are associated with deep water crabs or palinurids.

Neither the pelagic nor the deep water barnacles are of any assistance in determining the relationship to other faunal areas. The three species of the pelagic genus *Lepas* which occur in the Gulf are nearly cosmopolitan. Conversely, the species of the deep water genera, *Scalpellum* and *Verruca*,

are known from only a few localities and from relatively few specimens in both the Gulf and adjacent areas.

Many tropical species of littoral barnacles are represented in the Gulf. Some of these species, *B. calidus*, *B. declivis*, *B. stultus*, and *C. s. angustitergum*, are limited to the West Indies fauna; *B. galeatus* and *T. s. stalactifera* occur also in the eastern tropical Pacific; and the other species, *C. patula* and *P. hexastylos*, are widespread in tropical waters. The last two species, *B. galeatus*, which has also been found on the Atlantic coast as far north as North Carolina, and *B. calidus* have a wide range in the Gulf, whereas, the other species are limited to the Florida Keys.

The rest of the common littoral barnacles of the Gulf are important components of the littoral fauna of the Atlantic coast where the northern limit varies from Massachusetts (*B. a. niveus* and *B. eburneus*) to New Jersey (*C. fragilis* and *C. testudinaria*) and the southern limit from the Caribbean coast of South America (*B. eburneus* and *C. fragilis*) to southern Brazil (*B. a. niveus* and *C. testudinaria*). With the exception of *B. eburneus* these species occur in one or more other faunal provinces.

The littoral fauna of the Gulf, therefore, consists of a mixture of warm temperate and tropical species. One ubiquitous species, *B. improvisus*, also occurs in the Gulf; the western Atlantic range of this species is from Nova Scotia to southern Patagonia. All of the common littoral barnacles of the temperate waters of the Atlantic coast and none of the common boreal species (*B. balanoides*, *B. crenatus*, *B. balanus*, and *B. hameri*) occur in the Gulf, but many of the tropical species found in the West Indies have not been reported from the Gulf.

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THE MYSIDACEA AND EUPHAUSIACEA

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Very little is known of the mysid and euphausiid fauna of the Gulf of Mexico. Only three articles deal with the mysids of the region and only one with the euphausiids, together reporting not over a dozen stations mostly occupied before 1900 by the steamer *Albatross*. Tattersall (1951), in his review of the mysids of North America, reports the following species from this region either on the basis of previous records or specimens not previously reported:

Family LOPHOGASTRIDAE

Lophogaster americanus Tattersall.
Lophogaster longirostris Faxon.
Gnathophausia ingens (Dohrn).

Family PETALOPHTHALMIDAE

Petalophthalmus armiger Willemoes-Suhm.

Family MYSIDAE

Gastrosaccus dissimilis Coifmann.
Gastrosaccus mexicanus Tattersall.
Mysidopsis bigelowi Tattersall.
Metamysidopsis munda (Zimmer).
Mysidium integrum Tattersall.

Hansen (1915), in his similar review of the euphausiids of the U. S. National Museum, lists two species collected by the *Albatross* in 1885 and one species collected by the *Grampus* in 1889: *Thysanopoda pectinata* Ortmann, *Thysanopoda orientalis* Hansen, and *Euphausia tenera* Hansen.

All of the species of euphausiids and the species of the first two families of mysids reported are pelagic or bathypelagic forms and were found in the deeper water of the Gulf. The species reported from the family Mysidae are all neritic forms and were collected relatively close to land.

The shortness of this list should not be construed to be indicative of an impoverished fauna either in numbers of species or in numbers of individuals, but rather it should be seen as an indication of insufficient sampling. To catch these relatively large and active planktonts it is necessary to tow for them with large and rather coarse-meshed plankton nets; as many of the species exhibit diurnal migrations it is necessary to tow either at the surface after dark or in deeper water during the day. To capture many of the species of mysids it is necessary to sample the waters immediately above the mud and sand bottoms, for mysids are often hypoplanktonic and spend most of their lives hovering immediately above the bottom. When adequate sampling is carried out the number of species of both mysids and euphausiids can be expected to at least quadruple.

When the fauna of the Gulf is better known the "schizopods" will be found to be divisible into four major ecological groups:

1. *Epipelagic (or epiplanktonic) species.*—This group, living in or near the photic zone of the open sea, will include a few species of mysids but most of the species of euphausiids. The species probably will be found to be relatively widespread in the adjacent regions of the subtropical and tropical Atlantic at least, and possibly will be found to be circumtropical like *Euphausia tenera* listed above.

2. *Bathypelagic species.*—This group will contain both mysids and euphausiids but will be rich neither in number of species nor in number of individuals. Most species that will be found probably will have extremely wide ranges of distribution like *Petalophthalmus armiger* which is also known from off Ireland, the Gulf of Panama, the Gulf of Aden, the Bering Sea, and off Hawaii, to list a few of its localities of capture.

3. *Neritic species.*—This portion of the "schizopod" fauna will be composed mainly of species of mysids with the addition of some species of euphausiids. The distribution ranges of species in this group will be more narrow than those of the pelagic group; some at least will extend for thousands of miles along the coasts. Examples of the type of range are *Mysidopsis bigelowi* which is known to extend from Massachusetts to Louisiana and *Metamysidopsis munda* which extends from Chesapeake Bay to the coast of Brazil. Other species may have a more limited distribution.

4. *Hypoplanktonic species.*—This group, found living hovering above the bottom or temporarily on the bottom in the lower littoral zone and in the deeper waters of the continental shelf, are almost exclusively mysids of rather wide distributional range along the shore lines. As these species often migrate high enough into the water above the bottom to be captured by an ordinary plankton net, in the absence of exact data of capture, it is impossible to determine whether any of the known species of the Gulf are commonly hypoplanktonic.

A more thorough study of the mysids and euphausiids of the Gulf of Mexico probably will show that these rather prominent elements of plankton of the open sea and of inshore waters are essential food intermediates for commercially important fish, as they have been found to be in other regions of the world.

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STOMATOPODA

By Fenner A. Chace, Jr., *United States National Museum*

The stomatopod fauna of the Gulf of Mexico is very poorly known. There are several records from Key West and the Dry Tortugas, some from the west coast of Florida between Tampa Bay and Sanibel Island, as well as from the northern Gulf between Pensacola and Grand Isle, and a few from Galveston, the Gulf of Campeche, and Campeche Bank. In view of the limited collecting it is surprising to find as many as 13 species of stomatopods from the Gulf recorded in the literature. Preliminary examination of material recently added to the national collections, especially from the dredgings of the M/V *Oregon* of the Fish and Wildlife Service, indicates that several species will be added when the study of this material is finally completed.

The following list of species and the accompanying bibliography have been compiled largely from a manuscript synonymy of the stomatopods prepared and kindly made available by Dr. L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden, Holland. Without access to this invaluable summary of stomatopod literature the present survey would undoubtedly be less complete.

STOMATOPODS KNOWN FROM THE GULF OF MEXICO

Gonodactylus oerstedii Hansen, 1892.
Bigelow (1894); Gibbes (1850); McClendon (1911); Pearse (1932); Schmitt (1940); Sharp (1893).
Off Havana; Key West; Dry Tortugas. Also North Carolina and Bermudas to Brazil; Gulf of California to Ecuador.

Lysiosquilla excavatrix Brooks, 1886.
Anonymous (1942); Lunz (1935).
West of Charlotte Harbor, Florida (28 fathoms); Mobile, Alabama; Grand Isle, Louisiana. Also North Carolina.

Lysiosquilla scabricauda (Lamarck, 1818).
Anonymous (1942); Bigelow (1894); Lunz (1937); Sharp (1893).
Key West, Sanibel Island, Johns Pass, and Pensacola, Florida; Grand Isle, Louisiana; Galveston, Texas. Also New England to Brazil; West Africa.

Odontodactylus havanensis (Bigelow, 1893).
Bigelow (1893, 1894); Lunz (1937); Rathbun (1920).
Off Havana, Cuba; Key West; Dry Tortugas; Campeche Bank. Also Bahamas; Curaçao.

Odontodactylus nigricaudatus Chace, 1942.
Chace (1942).
Gulf of Campeche.

Pseudosquilla ciliata (Fabricius, 1787).
Lunz (1937).
Key West. Also Bermudas, Bahamas, and Florida Keys to Brazil; Indo-Pacific.

Squilla edentata (Lunz, 1937).
Lunz (1937).
West-southwest of Pensacola, Florida (120 fathoms).

Squilla empusa Say, 1818.
Anonymous (1942); Bigelow (1893, 1894); Faxon (1896); Lunz (1937); Rathbun (1893); Sharp (1893).
Sanibel Island and Pensacola, Florida; Grand Isle, Louisiana; Galveston Bay, Texas; northern Campeche Bank (84 fathoms). Also New England to Brazil; West Africa.

Squilla intermedia Bigelow, 1893.
Bigelow (1893, 1894).
Off Mississippi Delta (68 fathoms). Also Little Bahama Bank; Puerto Rico.

Squilla neglecta Gibbes, 1850.
Lunz (1937).
Sanibel Island, Florida. Also North and South Carolina.

Squilla rugosa Bigelow, 1893.
Bigelow (1893, 1894).
Off Charlotte Harbor, Florida. Also Isle of Pines, Cuba (subspecies ?).

Squilla, sp. [*S. prasinolineata* Miers, 1880, not Dana, 1852].
Ives (1891).
Silam, Yucatán. Also Brazil.

The present limited knowledge of the distribution of stomatopods, both within the Gulf of Mexico and elsewhere, does not permit any definite zoogeographical conclusions. Five of the thirteen species recorded from the Gulf (*Gonodactylus oerstedii*, *Lysiosquilla glabriuscula*, *L. scabricauda*, *Pseudosquilla ciliata*, and *Squilla empusa*) are known to have extensive ranges, at least from the Carolinas to Brazil. Three of these

which are comparatively common elsewhere have been found thus far in the Gulf area only in the western approaches to the Straits of Florida. It may be of interest that the two species which seem to be most generally distributed in the Gulf (*Lysiosquilla scabricauda* and *Squilla empusa*) are the only ones also recorded from West Africa. Of the species with more restricted ranges, *Lysiosquilla excavatrix* and *Squilla neglecta* are known outside of the Gulf only from the Carolinas; *Odontodactylus havanensis*, *Squilla intermedia*, and *Squilla rugosa* (subspecies ?) have been recorded from the Bahamas-West Indies region; *Squilla prasinolineata* [Miers, not Dana] is a Brazilian species not yet found north of Yucatán; and *Odontodactylus nigricaudatus* is at present represented only by the type specimen from the Gulf of Campeche.

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DECAPODA OF THE GULF OF MEXICO

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GENERAL PHYSIOGRAPHIC REGIONS

The decapod Crustacea of the Gulf comprise a division roughly arranged in four, environmentally limited, large groups.

The first of these groups is made up of land forms living more or less on the edge of the salt water and spending part of their life in the sea. This group consists largely of members of the families Gecarcinidae, Grapsidae, and Ocypodidae. Their habitat is conditioned by the nature of the Gulf shores, which in the eastern part of the region under discussion (southern Florida) and on the southern rim are coral shores or limestone, but for the rest mostly sandy or muddy. The genus *Cardisoma*, the commonest representative, becomes in parts of this region a very conspicuous inhabitant of the shores and even of the inland areas. The spot distribution of this particular genus, from Florida to Texas, is a matter of considerable interest. Of its occurrence on the western border of our area, nothing is known. Other widely distributed forms are the family Grapsidae (genus *Sesarma* with subgenera), and the fiddler crabs, ghost crabs, and other Ocypodidae. Some of the genera of this family, such as *Uca minax*, invade brackish and even fresh water shores, though they are seldom found very far from water, even when not breeding.

The second major group is the fauna of the littoral, by far the best known and perhaps the largest segment of the decapod population of the Gulf. The northeastern portion of the northern Mexican coast, especially Yucatán, shows the 1,000-fathom line far off shore, though the shelf from the 100-fathom line is very steep. In the western Gulf (400-foot contour line) the drop is the steepest. The shallows extend farthest out on the north (Louisiana, Mississippi) and east (Florida) and on the northern shore of Yucatán. The littoral therefore comprises a zone of greatly varying width. The spread of the decapods over this area and the ecological niches that may have developed locally are matters of great interest to our general problem.

Roughly, the littoral here is composed of four major habitats, of which two are very similar.[1] There is first (region 1) the shore bordering the mouths of the great rivers. These shore lines are heavily fringed with the muddy deposits of river deltas. The rivers of the southern portion and also of Florida are much shorter, and there is a much lesser volume of deposited material than in the larger northern and western ones, chief among which are the Rio Grande, the rivers of the Mississippi Delta, and the Alabama drainage. The northern shore line appears fairly constant; but some observations would seem to indicate at least two faunal breaks—one at the Mississippi and perhaps a second somewhere between that point and the Texas-Mexico line, which seem to be other than purely climatic. Along the river mouths and up their muddy channels are to be found many mud crabs, definitely the richest single decapod element. Many species of *Panopeus*, *Hexapanopeus* and *Rithropanopeus*, *Eurytium*, and other related genera abound here. In general, we may expect this fauna to differ little from that of the muddy bays to be discussed later (region 3). There is a slightly more active flow of the water and more direct influence of winds, tides, and currents than in the back bays. Probably the single greatest variant is the periodic great alterations in salinity in "high water" years; and this does not seem seriously to affect the decapod population. A very bountiful fauna inhabits the muddy river mouths and tide flats. There is also an additional ecological factor in the slow run-off, which has resulted in man-made artificial microhabitats in the form of jetties, where dwell the rock crabs, along with many other normally rock-dwelling invertebrates that have adopted this territory.

[1] We shall use the rather indefinite term "region" to indicate each of these habitats.

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The second region (region 2) of the littoral is composed of the shores of the bars or islands between these run-offs; these areas vary greatly in stability and extent, but appear rather constant in structure and physical nature. But, as mentioned earlier, this apparent constancy is deceptive; a more intensive study of the Brownsville region and the Texas shore line immediately north and east reveals the disappearance of the marsh so characteristic of the Mississippi-Alabama-Louisiana shore line and its replacement by much more sandy shores facing the sea. This can be seen from any topographic map. There have been no comparative faunal studies of this region but such studies might well be expected to reveal an associated faunal break. Intensive studies of a few limited localities show the species of a single genus, such as for example, *Callianassa*, which occur on the ocean side of a bar in the northern Gulf, are definitely more closely related to those in similar habitats in more southern areas than they are to those found along shores with different soil composition in the same climatic zone. Thus it appears that along the northern Gulf, at least, temperature is not a strictly limiting factor.

In general, the common families of region 2 are the Callianassidae, Albuneidae, Hippidae, and some representatives of the Paguridae; the Portunidae represented by the ubiquitous *Callinectes* of many species, and others of that family; a few Pinnotheridae along the sand bars, especially on the open or widely exposed shores; and in slightly sheltered regions and small transient tidal pools, such Palaemonids as *Macrobrachium* and *Palaemonetes*.

The east coast of Mexico is not too well known; although it differs, as we go south, from the Texas shore line. Limestone, coral sands, coral reefs, and actively growing corals, with strips of rocky cliffs of laval origin, prevail. The underlying rock is limestone with much calcareous sand mixed with coral along the shore line. Theoretically, the coral provides the habitat for the crustacean forms which might be expected to replace here the rocky-shore species of other sections. What we might consider the southern rim of the Gulf, namely, the northern shore line of the Yucatán Peninsula, is another region not adequately explored nor described. It may be presumed, however, that such reefs as are present would show a more constant and consistent animal life than is to be found in similar habitats of the northern Gulf, since there is less depositional modification. Here is another key locality for important further study of the Gulf littoral.

Region 3 of the Gulf littoral comprises scattered shallow bays with muddy or occasionally shelly bottoms. This condition is found along the northern and western Gulf. Here there is a typical mud-bottom fauna living at depths of from a few to 20 or 30 feet, and consisting of many Xanthids, some of the family Porcellanidae, especially *Petrolisthes*, species of Inachidae, Palaemonidae, and Crangonidae, and a few of the families Calappidae, Parthenopidae, and Maiidae. Other Xanthids are distributed along the muddy shores of these embayments, where their burrowing often completely riddles large areas of tidal mud flats.

There is a further gap in our knowledge: the fauna of large parts of northern Cuba. From the general topography we would expect a rich fauna on these shores. The forms from the northern shore of Cuba as far as they are known belong more to the Caribbean—more precisely, the West Indian fauna—than to that of the Tortugas and the Florida Keys. But this may be questioned; the picture is not clear-cut, again for lack of records.

Region 4 is the reef fauna of western Florida and the Keys. As suggested above, it may be supposed that we would find here a fauna comparable to that of the West Indies; and as far as the fairly comprehensive studies from the Tortugas show the forms found here are indeed similar to those of the larger islands, such as Puerto Rico, which have been fully studied. They grade into those of northern Cuba. Comparison of this material with that from central and northern South America should show many definitely tropical characters.

The third major group comprises the fauna of the deeper Gulf. On the whole, this fauna is known only from isolated samples of the population since thorough study is wanting. Explorations so far have not been extensive, though in the neighboring West Indies some records have included material from considerable depth. The species found here might presumably be most constant, since temperatures vary less than elsewhere in our general territory except, perhaps, in that part of the Gulf floor which is under

direct influence of the subterranean river deposits. The forms so far described or listed from this region, though not as far as is known limited to it, include the Peneidae which are of considerable economic interest,[2] some of the Porcellanidae, Pagurids of several genera, Inachidae, though not of the same species as those found in the mud flats, and again, Portunids.

The fourth group to be considered is the drift invaders, chiefly from the south, brought in from the south and southeast by winds, tides, and ocean currents either through the Florida Straits or the Yucatán Channel. This group comprises plankton, with larval stages of decapods included, the identification of which has hardly been touched; also, the species that as adults, even egg bearing, are domiciled on the sargassum drift and found in considerable abundance whenever weather conditions in the far and nearer Gulf bring seaweed into the shore. In this category are to be found many of the free-living of the lower crustacean decapods dependent on the plant drift, larvae and adults, especially of the families Portunidae, Parthenopidae, Palaemonidae, and Maiidae.

Thus, examination of our records of the decapod Crustacea of the Gulf of Mexico indicates very clearly large gaps in our knowledge. These gaps are less evident along the northern shore and the Florida Keys than along the eastern part of Mexico and Yucatán. However, since the physical environment falls into the several general types as outlined, we may hope to find a fairly close correlation of the fauna with environments. This correlation will probably go no further than to genera.

COMPARISON OF FAUNAS

Of all the quantitative and intensive studies there are very few which give us a clue as to the general sources or relationships of the Gulf decapod fauna. The big question is: is this fauna largely derived from the tropical forms coming into the Gulf through the Florida and Yucatán Straits, or, on the other hand, does it show more temperate zone characters? Adequate answers are not forthcoming from presently available data, but we may at least glance at the two sets of fairly comparable records: (1) Schmitt's and Rathbun's Puerto Rican material, (2) material from the northern Gulf from the Louisiana State University Laboratory at Grand Isle, Louisiana, and Hedgpeth's Port Aransas, Texas, collection, lumped together. Schmitt's and Rathbun's material is what we may think of as typical West Indian tropical. The fauna of the northern Gulf will be used for comparison, since that area has been worked more intensively than other regions, and since drift from the tropics clearly reaches that shore (sargassum inhabitants).

Schmitt's and Rathbun's collections comprise 40 families, 171 genera, and 315 species. The northern Gulf collections referred to above are represented by 26 families, 66 genera, and 113 species. Of these, 21 families and 41 genera are common to both groups. It may be that some lack of agreement between the two sets of records is due to collecting techniques. However that may be, numbers show that if this comparison is to have any validity the faunal records of the northern Gulf need to be expanded.

It appears from such records as are available that the northern Gulf collections contain two families (one genus in each), usually considered temperate zone families, and not recorded from Puerto Rico. Further, it appears that in those families common to both collections, there are five genera of the shrimp and shrimp-like crabs and one genus of the Brachyura which occur only in the northern Gulf. On the other hand, there are 13 families of Anomura and Macrura and 6 of Brachyura from Puerto Rico which have not been reported from the northern Gulf. (Whether these are all truly tropical families may be questioned.)

The materials reported here indicate a large field for further taxonomic, ecological, and distributional studies on the decapod Crustacea of the Gulf of Mexico.

REFERENCE COLLECTIONS

The specimens serving as a basis for comparison for future students of the Gulf decapods are scattered rather widely. In this country the most important are:

The collections in the U. S. National Museum. Of these may be mentioned those of Schmitt and Shoemaker from the Tortugas, those of Schmitt (on Walter Rathbone Bacon scholarships) from two extended South American explorations, and other smaller ones.

[2] See article on shrimps by M. J. Lindner and W. W. Anderson in this book, pp. 457–461.

The collections from the United States Bureau of Fisheries made at various times by the *Albatross* the *Fish Hawk*, and the *Grampus*. The collections made by the Fish Commission in the Atlantic in 1838–42 and in the North Pacific, 1853–56.

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BIOLOGY OF COMMERCIAL SHRIMPS

By MILTON J. LINDNER and WILLIAM W. ANDERSON, *Fishery Research Biologists, Fish and Wildlife Service*

About 140 million pounds of shrimp were taken from the Gulf of Mexico in 1949. In the Gulf there are four commercially important shrimps: the common, white or lake shrimp, *Penaeus setiferus*; the grooved, Brazilian, pink and brown shrimp, *P. duoarum* and *P. aztecus*; and the sea-bob, *Xiphopenaeus kroyeri*. Of these, *P. setiferus*, during the middle 1930's, accounted for about 95 percent of the catch. At that time the fishery in the Gulf proper extended from St. Marks, Florida, with gaps, to Brownsville, Texas. Now, the fishery extends along almost the entire perimeter of the Gulf, and *P. aztecus* and *P. duoarum* have become progressively more important. Probably more than one-third of the 1949 catch was of these two species. Since we know more about *P. setiferus* the remarks that follow pertain to this species only and just for the northern Gulf of Mexico.

P. setiferus is most abundant in areas that are characterized by having an inland, brackish marsh connected by passes with an adjacent shallow offshore area of relatively high salinity and mud or clay bottom. The offshore characteristics seem to be required by the adults and probably also the larvae, while the inland marshes appear to be required by the post-larval pre-adults. The adults are rarely found in abundance in the Gulf of Mexico in depths greater than 30 fathoms. The pre-adults inhabit brackish water and at times are found in water that is almost fresh.

The females do not carry the eggs after fertilization but deposit them directly into the water. Some time prior to the emission of the eggs (time not known) the female has a spermatophore attached to her by the male. The eggs upon emission are fertilized by the sperm contained in the spermatophore. A female will lay about 500,000 eggs at each spawning, and it is probable that there is more than one spawning in a season.

As in other peneids, the first larval stage upon hatching from the egg begins as a nauplius. The larval stages are represented by at least five naupliar, three protozoeal and two mysis stages.

Most, if not all, spawning takes place at sea and not in the estuarine inland waters. Either during or shortly after the larval stages the young shrimp move from the waters of the Gulf to the estuarine waters. Growth is rapid in these estuarine waters. When the young are about 50 mm. in total length (from tip of rostrum to end of telson) they begin to appear in abundance on the estuarine commercial fishing grounds.

The young first appear in the estuarine fishing grounds in June or July, depending upon the area, and by August they have begun to make their appearance in the waters of the Gulf. Generally, in the estuarine waters there is a gradient in size of the shrimp, smaller shrimp occurring in those waters farther inland and larger shrimp in those waters nearest the Gulf. This gradient in size appears to be associated more closely with locality than with salinity.

As the young increase in size they gradually move toward the open waters of the Gulf (fig. 70). The movement of shrimp from the inland waters to the open waters of the Gulf is intensified by the decreasing water temperatures during the fall. As the waters warm in the spring the larger shrimp which are in the open waters of the Gulf mature rapidly and spawn. The smaller shrimp which have wintered in the estuarine waters or in Gulf waters close to shore grow and mature rapidly but spawn later.

Spawning occurs, and appears to be continuous, from at least the latter part of March through September. Apparently there are two major peaks of spawning success. The first peak can be attributed to April in Louisiana and generally June near Aransas Pass, Texas. Growth is rapid and the young from these spawnings produce the fall "run" of shrimp. The spring "run" of shrimp is produced by the second peak of spawning success which appears to result from

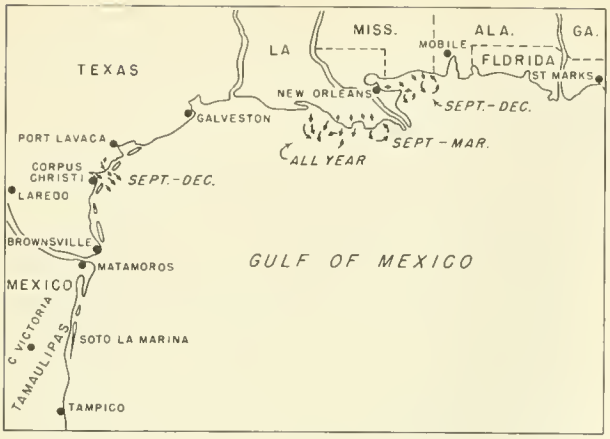

FIGURE 70.—Small shrimp (up to 13 cm.) movements of marked individuals.

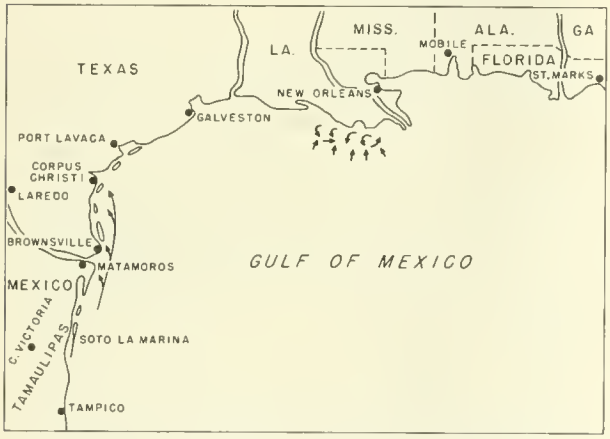

FIGURE 71.—Large shrimp (13 cm. and larger) spring movements of marked individuals.

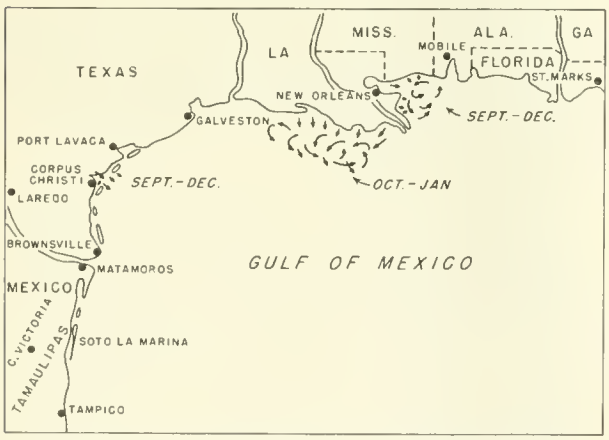

FIGURE 72.—Large shrimp (13 cm. and larger) fall and winter movements of marked individuals.

August or September spawning, both in Louisiana and in Central Texas. The shrimp from the first successful spawning have left the estuarine nursery grounds by midwinter. The young from the second successful spawning generally remain during winter in the estuarine waters and the immediately adjacent inner littoral waters.

The growth of the shrimp is quite rapid during the warm months of the year. From the time of hatching until they reach a length of about 120 mm. the shrimp apparently increase at a rate that averages more than a millimeter each day. This rapid rate continues until about the end of October when growth stops or almost stops, apparently as a result of temperature changes. From about the end of October until the end of February or of March, depending upon the locality, there is little or no growth. In the spring, as the water temperature increases, the shrimp again resume their rapid growth.

From central Texas south there is a definite possibility of migration. In the spring, based upon specimens marked in Mexico, there is a northward movement of shrimp. By inference, and from the time of the first successful spawning, but not based upon marked specimens, it appears highly probable that shrimp from the central and southern part of Texas may move south to the coast of Mexico during the fall and early winter, probably comparable to the movement along the South Atlantic coast of the United States.

In the northern portion of the Gulf of Mexico the wanderings of the shrimp can better be described as movements rather than as migrations (figs. 71, 72). The young gradually move from the estuarine waters to those of the Gulf. Once in the Gulf they appear to mill about like grazing cattle. However, as the temperatures drop during winter the shrimp tend to move a little farther offshore, and as the waters warm in the spring they tend to move back closer toward shore.

The movements of the shrimp are associated with spawning and with temperature. The normal spawning movement is offshore. During winter, in some localities, the movement becomes coastwise because of temperature gradients. Along the northern part of the Gulf of Mexico, warmer winter waters which the shrimp seek are generally found in a belt between the 5- and 30-fathom lines.

In this section of the Gulf, because of the east-west direction of the coast line, there is no appreciable coastwise gradient in temperature. There is, nevertheless, a slight offshore gradient and apparently the shrimp take advantage of this gradient.

Along the western side of the Gulf there is a southward temperature gradient during the winter, and it is probable that there is a southward movement of shrimp from central and southern Texas into Mexico during this season.

The mortality rate is high and although some undoubtedly survive into their second year, for all practical purposes the shrimp can be considered an annual.

In order to manage the shrimp supply properly we must have considerably more knowledge than we have at present. We must know more about the relationship between the abundance of shrimp and their food supply; the effect of thinning or not thinning the population on the nursery grounds; the natural and fishing mortality rates, and the possible competitive action between the white and the grooved shrimps. In addition to these, there is a considerable gap in our knowledge between the time the eggs are laid until the shrimp appear on the nursery grounds. Our present information on this phase of the life history of the shrimp is indeed sketchy. What, for example, causes the apparent peaks in spawning success and what is their significance with respect to the management of this resource? The story of the shrimp is by no means a closed book. Our information has now arrived at the stage where approaches can be made to many important practical problems affecting the relationship between man, the environment, and the shrimp.

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BIOLOGY OF THE SPINY LOBSTER[1]

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The spiny lobster, or crawfish, of the Gulf of Mexico and the Caribbean belongs to a family of shellfish which is related to the true lobsters and which is to be found in the warmer seas throughout the world. Some members of this family are commercially valuable and support fisheries in South Africa, Australia, California, Hawaii, Japan, and the Caribbean region, including Florida and the Bahamas where they are variously known as rock lobster or spiny lobster, sea crayfish, langouste, and langosta. They are referred to as spiny lobsters because of their similarity to the true or northern lobsters from which they are distinguished by the presence of numerous spines on their bodies and legs and by the absence of large claws. Whereas in the true lobsters the edible meat is mainly taken from the claws, the chief edible portion of the spiny lobster is the tail muscle. Although related, spiny lobsters must not be confused with the smaller fresh-water shellfish utilized commercially in a number of countries under the name of crayfish. For this reason, the term spiny lobster is to be preferred.

Color varies with age and the type of bottom upon which the animals live. Brighter, greenish, or sandy colored animals are usually found on sandy bottom or in shallow water. Darker animals with a greater proportion of blue and brown are found in darker bottom or in deeper water.

The Gulf of Mexico species, *Panulirus argus* (Latreille), is found on the western Atlantic shores from Rio de Janeiro, Brazil, throughout the West Indies to Florida, and rarely as far north as North Carolina. Although occasionally present in other parts of the Gulf of Mexico, they are only abundant in the Florida Keys.

Small numbers of related species are occasionally taken in the commercial catches but usually pass unnoticed. *Panulirus laevicauda* Latreille and *Panulirus guttatus* Latreille are most frequently encountered in this manner in Florida and the West Indies. Others not yet taken in the Florida catch but which are likely to occur rarely are *Palinurellus gundlachi gundlachi* (Von Martens), *Palinustus truncatus* (H. Milne Edwards), and *Justitia longimana longimana* (H. Milne Edwards). Species of the genus *Scyllarides*, belonging to a related family, are taken occasionally in the Gulf of Mexico.

Sexual Characters.—Sexes may readily be distinguished by the following characters. The tips of the fifth pair of walking legs in the male terminate in a single, simple claw similar to those of the other legs. In the female, the fifth leg terminates in a pair of projections which act as pincers used for preening the eggs where they are attached to the under surface of the tail. The male also differs in the presence of swollen sexual openings at the base of the last pair of walking legs. The female openings are much smaller and are at the base of the third pair of legs. A further distinction lies in the swimming legs. In the males these end in a single, leaflike joint, whereas, in the female, they are branched. In the first two pairs these branches are leaflike, while in the following legs the inner branch is a rod-like joint to which the eggs become attached.

Habitat.—The spiny lobster is most active at night when it moves about in search of food. During the daytime, it is usually hidden under rocks, sea grasses, sea fans, large sponges, or other marine growth, with only the whips projecting. There is also a tendency to avoid very strong currents and muddy bottom. Grassy bars with rocky heads and an abundant supply of small shell creatures and worms, especially if protected from excessive wave action, are likely places to find new lobster grounds. While they are usually caught in less than 30 feet of water, it is definitely known that spiny lobsters exist in much greater depths where there is rocky bottom. Movement is usually carried out by walking forward on the

[1] Contribution No. 110 from the Marine Laboratory, University of Miami

legs, but occasionally, by quickly bending the tail, the animal will move backward rapidly to avoid danger.

Food and Enemies.—The spiny lobster has a wide range of food and is frequently a scavenger. Examination of the stomach shows small mollusks, such as young conchs and pelecypods, worms, and occasionally, small Crustacea. Seaweed is frequently found in the stomachs but may not necessarily be of food value. Spiny lobsters will also eat the fresh and dried meat of fish. Food is usually detected by the lobster at some distance by means of a chemical sense in the whips.

In the early stages of development, the spiny lobsters are small, transparent creatures which drift in the water. In these stages they are eaten by a great variety of fish and plankters. After they change into the adult form, but while they are quite small, they crawl among the rocks or grass and are frequently eaten in large numbers by groupers, snappers, and other bottom fish. The older lobsters, even up to a large size, are food for sharks, groupers, and jewfish.

Breeding Habits and Life History.—At some time between February and July, mating occurs at which time the male extrudes a viscous fluid from the swollen openings at the base of the last pair of walking legs. This fluid becomes attached to the under surface of the female between the last three pairs of legs and rapidly hardens on the outside to form a dirty-white or gray-black substance known as the sperm sac.

A short time after the mating act, the females lay their eggs, or berry, which become attached to the paddles under the tail. The eggs are a bright orange-red in color and about $\frac{1}{32}$ inch in diameter. They are fertilized by spermatozoa which the female releases from the still soft inside of the sperm sac by scratching with the tips of her legs. The number of eggs varies with the size of the lobster. In the case of a 9-inch animal, the number is about 500,000 forming a berry-like mass.

Most of the females migrate into deeper water while the eggs are incubating and hatch them during the summer months within 3 weeks after laying. The majority of egg-bearing females are found in April. Some females may mate later than others and, as a result, a small number may still be found with eggs as late as November. The old or spent sperm sac is also found in occasional individuals during every month of the year. Most females, however, have completed breeding by the beginning of July. After releasing the eggs, the females begin to return to shallower water.

A small number of females under 7 inches in length, measured from the tip of the telson to a point between the "horns," are found carrying eggs. These have a cape length of under 2 inches and a weight of under ½ pound. The majority, however, do not appear to breed until they reach a body length of 8 inches, corresponding to a cape length of 2½ inches and a weight of ¾ pound (Smith 1951).

The egg of *Panulirus argus* hatches directly into a phyllosoma larva (Lewis 1951). This is a flat leaflike planktonic form with long legs and prominent stalked eyes. Eleven stages of development are recognizable during the planktonic existence which appears to last over a period of as much as 6 months. The larvae grow from about 2 mm. in length to about twice this size. During this period they are carried considerable distances by currents and are sometimes found in plankton hauls taken in the open ocean.

No information is available regarding the behavior of larvae of *Panulirus argus*. It is reported, however, by Von Bonde and Marchand (1935) that the early planktonic stages of the South African species react to light so as to appear at the surface during nighttime and to retire to deeper water during daylight hours. In the Australian species the final stages before metamorphosis are found at the surface.

Migrations.—As a result of tagging experiments in the Bahamas and in Florida, it is known that the spiny lobster is able to migrate over considerable distances. Individuals have been recaptured as much as 100 miles from the point of release after a lapse of a little more than 100 days.

At all times of the year, lobsters may undergo mass movements alongshore, apparently in relation to the food supply. They also tend to move inshore immediately after stormy periods. At times, offshore movements seem to be associated with prolonged calm or warm weather, but mass movements have also been observed with no accompanying change in physical conditions. These may also be related to a scarcity of food.

Although these are insufficient experimental data to draw any definite conclusions, the observations of fishermen upheld general observations regarding seasonal movements associated with breeding habits. (Dawson and Idyll, 1951.)

During the months of February to April, the lobsters tend to collect in certain inshore areas while mating. During April to June, the females move into deeper water where the eggs are laid and return again during July and August. Spiny lobsters also tend to move offshore during the cold months of December and January. There is reason to believe, however, that spiny lobsters are present at all times of the year in deeper water wherever there is protection in the form of rocky heads or marine growth.

Molting.—At intervals, the spiny lobster casts its shell and grows a new one. Molting is evident in some lobsters at all times of the year. Observations made in the Bahamas show that the majority of males and young females are found molting during the months of April to June and again during October to December. The mature females molt during early spring before the start of the breeding cycle, and sometimes during August after they have shed their eggs. Only the smaller, immature females molt during June. Molting probably takes place following periods of abundant food supply and is partially dependent upon temperature.

Prior to molting, the spiny lobster seeks the shelter of rocks and ceases to feed actively. For this reason, the number of molting individuals in the ordinary type of trap does not truly indicate the percentage undergoing molt. After a period varying from a few hours to a few days, the old shell cracks along definite lines and becomes dislodged first from the cape region and then from the tail. The new shell is in place beneath the old one before molting, but it does not harden completely for at least a week.

Immediately after losing the old shell, the lobster has been found to absorb considerable quantities of water. This accounts for the rapid increase in size prior to hardening of the new shell. From the time when cracks first begin to appear in the old shell until the new shell no longer feels soft when compressed in the hand, molting takes a little more than 2 weeks.

Growth Rate.—Studies of growth rate have been based upon the direct measurement of captive individuals, length frequency analyses of the catch, and by a comparison of molting frequency with growth between molts. Although none of these methods have given conclusive results, they indicate that growth of the spiny lobster when about 1 pound in weight is somewhat greater than 1 inch per year.

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CHAPTER XV
MOLLUSKS

MOLLUSKS [1]

By HARALD A. REHDER, *Smithsonian Institution* [2]

The Gulf of Mexico is, chronologically speaking, probably the least known body of water adjoining the United States, and the mollusks of its shores are as yet only imperfectly known. This is particularly the case with the area between Cedar Keys on the Florida coast, and Sabine Pass on the Louisiana-Texas border, and with the part of the coast line stretching between the mouth of the Rio Grande and the vicinity of Veracruz.

The littoral fauna of the Gulf of Mexico may be divided into two elements that inhabit different geographical areas. There is first the tropical element found on the Florida Keys and north on the Gulf side of Florida to about Tampa Bay, the northwest coast of Cuba, and the Mexican coast from Cabo Catoche on Yucatán north to the vicinity of Corpus Christi, Texas (and possibly to near Matagorda Bay). This area forms the southern limit of the Gulf of Mexico and is the only part of the Gulf area in which living, fringing reef corals are found. Joubin's (1912) representation of coral reefs in Tampa Bay is obviously an error.

North of this tropical Caribbean area the fauna takes on a more temperate character, showing an obvious relationship with that of the zoogeographical province generally known as the Carolinian. The physiography of this area is also in general different from that of the more southerly shores. It is a region characterized mainly by sandy beaches either on the mainland or on low coastal or barrier islands that are separated from the mainland by shallow lagoons or bays with passes or inlets between the individual islands. No coral reefs are found in this area, although there are submerged coral banks off the coast as far north as northern Florida.

The mollusks of the deeper waters of the Gulf show, mainly, a relationship with the West Indian fauna but have also some affinities with those of the deeper waters off the southern Atlantic coast of the United States.

PAST WORK DONE IN THIS AREA

GENERAL

The first publication that gave a list of the mollusks found along the entire Gulf coast and discussed their geographical ranges was Dall's (1889) catalog, reprinted, with additions, in 1903. Dall divided the southeastern coast into 10 geographical districts. Three of these districts covered the area included in this report: Florida Keys, from the Keys north to Charlotte Harbor, West Florida, from Charlotte Harbor to the Mississippi Delta, and the deeper waters of the Gulf east of longitude 90°, and Texas, from the Mississippi Delta to the Rio Grande, and the deep waters south to Yucatán. The broad extent of the Texas district has led to the inclusion, in later lists, of many species as being found in Texas that have not as yet been recorded from the waters of that State. This is true, for instance, of Johnson's (1934) list mentioned later.

Maury (1920, 1922) published a catalog of the recent mollusks of the Gulf of Mexico in which were included some Tertiary species. Johnson's (1934) List of the Marine Mollusca of the Atlantic Coast from Labrador to Texas came out posthumously. This check list, though not always, indicates those species found along the shores of the Gulf of Mexico.

FLORIDA

The west coast of Florida is better known from a malacological standpoint than any other section of the area under discussion. Numerous catalogs and annotated lists covering this area were published in the seventies and eighties: Calkins (1878, 1880), Dall (1884), Simpson (1887, 1889). Melvill (1881) gave a list of the mollusks of Key

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[2] I would like to acknowledge the helpful suggestions received from Prof. T. E. Pulley of the University of Houston.

West, enumerating 123 species. In more recent years several papers have been published dealing with the mollusks of Sanibel Island, near the mouth of the Caloosahatchee River, in Lee County; Clench (1923, 1925) listed 89 species, while Haas (1940) gave ecological notes on many of the species found here. In the last few decades some collecting has been done along the northwestern coast (Lyman 1942; Schwengel and McGinty 1942). The most complete work on the mollusks of western Florida is that by Louise Perry, Marine Shells of the Southwest Coast of Florida, 1940, in which she describes 346 species most of which are illustrated.

ALABAMA-LOUISIANA

The published records for this area are fewer than for the Gulf coast of Florida or for Texas. The first faunal list I have been able to find is that by Vanatta (1904) who published a list of mollusks from Horn Island, Mississippi. Cary (1906) enumerated 73 species from various places along the Louisiana coast from Cameron in the western part to the Chandeleur Islands in the east. Whereas in Cary's list the proportion of gastropods to pelecypods is 32 to 38, in the Horn Island list the proportion is 3 to 32. This seems to suggest that the shells of Horn Island were gathered almost exclusively along the outer beach and that further search on the lagoon side of the island would bring to light further species. In 1929, Clench listed 23 species from various localities in southern Louisiana in the Mississippi Delta region. Burkenroad (1933) enumerated 9 species of pteropods from the waters of Louisiana. The most recent list of Louisiana shells (Harry 1942) gives 93 species from the vicinity of Grand Isle and Barataria Bay. This report, the result of 12 years collecting by members of the staff of the Louisiana State University Marine Laboratory staff there, shows how impoverished the fauna is in this part of the Gulf in comparison with that of the regions farther south on both sides of the Gulf.

TEXAS

The first enumeration of the mollusks of this part of the Gulf, and indeed of any part of the area covered by this report, was that published by Ferdinand Roemer in his work on Texas (Roemer 1849). Out of 54 species he listed from the island of Galveston 7 were new species described by R. A. Philippi. Singley (1893) gave an extensive list of the marine mollusks of the Texas coast, listing 342 species. This contribution, being based in part on Dall's (1889) catalogue, contained many species for which no records from the waters of Texas proper are known. Mitchell (1894) published, privately, a list of Texas marine shells enumerating 81 species. The list was based on his own collecting and dealt mainly with the mollusks of the Matagorda–Corpus Christi Bay area. Strecker's (1935) list of Texas marine shells appeared posthumously; it contained 188 species, a number of which were not in Singley's list. As an appendix Strecker gave a list of 176 species said by Dall to come from the Texas district but for which Strecker had no specific localities. Stenzel (1940) published a list of 56 species from Point Isabel, Texas. A considerable amount of ecological work is being carried on at the present time by workers at the Institute of Marine Science at Aransas Pass (Hedgpeth, 1950; Whitten et al., 1950) as well as at the laboratory of the Texas Game, and Fish Commission at Rockport. Recently, Pulley (1949 and 1952) published on the mollusks of the Texas coast. His 1952 paper is a comprehensive one, in which he has included, with appropriate comments, those species previously recorded from Texas, but not known to occur there.

MEXICO

Only a few papers have been published on the mollusks of the east coast of Mexico. Baker (1891) listed 216 species from Veracruz, Silam, Progreso, and Campeche (the last three localities are on the peninsula of Yucatán), and Hinkley (1907) enumerated 47 marine shells from the vicinity of Tampico.

CUBA

The older works on Cuban shells, such as those by d'Orbigny and Arango, gave no specific localities for the marine mollusks. In the Catalogo de los Moluscos de Cuba, Aguayo and Jaume (1947–52) published some records from the northwest coast of Cuba. Henderson's (1916) book contains, also, a good picture of the northwestern coast of Cuba, although he gives no list of mollusks. Little collecting seems to have been carried out along the part of the Cuban coast between Habana and Cabo San Antonio, a region that should be very rich in mollusks.

DEEPER WATERS

The first work on the fauna of the deeper waters of the Gulf of Mexico was carried out in 1878 by the United States Coast Survey steamer *Blake* under the direction of Professor Alexander Agassiz. The mollusks gathered during this cruise were reported on by Dall (1886–89). Subsequently, the steamer *Albatross* of the United States Fish Commission made numerous stations in the eastern part of the Gulf, the results of which have been referred to in various scattered papers. More recently, the Fish and Wildlife Service vessels *Pelican* and *Oregon* have been carrying out investigations in the Gulf of Mexico in the course of which they have gathered many interesting mollusks which have been only partly reported on. The commercial shrimp fishermen have been initiated by the amateur shell collectors into the practice of saving the mollusks brought up in their nets, and in this way they are contributing many interesting finds. A preliminary report on some of these mollusks has recently been published by Rehder and Abbott (1951).

ECOLOGY

Under this heading are listed what seem to be the most important biotopes present in the littoral zone of the Gulf of Mexico. No attempt has been made to go into a detailed description of the various facies, zones, and associations.

Some of the species listed as occurring in one province or in one kind of habitat may, of course, be found also in other areas. It should likewise be pointed out that because of the lack of careful collecting along much of the coast line of the Gulf the extent and exact position of the transition areas between the Caribbean and Carolinian provinces is at the present time still largely a matter of speculation. This is especially true of the fauna of the moderate depths between the shore and the deeper waters.

CARIBBEAN PROVINCE

This zoogeographical area includes the northwest coast of Cuba from Cabo San Antonio to Habana, the west coast of Florida from the Dry Tortugas and Key West north to probably Tampa Bay (the northern limit of this province is somewhat doubtful here but lies somewhere between Sanibel Island and Cedar Keys), and the coast of Mexico from Cabo Catoche to the vicinity of Port Isabel, Texas, and possibly beyond to Corpus Christi Bay.

As is to be expected, the mollusks of this area show an obvious relationship with those of the West Indies and the entire Caribbean region.

The list of species has of necessity been taken largely from our knowledge of the Floridian molluscan fauna. An interesting and more extended discussion of these associations can be found in a report by Bartsch (1937).

1. Coral reefs, rocky outcrops, and jetties:

Here we find a rich fauna of which I list only a few species.

Acanthopleura granulata Gmelin.
Acmaea pustulata Helbling.
Fissurella cayenensis Lamarck.
Astraea americana Gmelin.
Nerita peloronta Linné.
Nerita versicolor Gmelin.
Nerita tessellata Gmelin.
Littorina ziczac Gmelin.
Tectarius muricatus Linné.
Cerithium literatum Born.
Batillaria minima Gmelin.
Thais rustica Lamarck.
Cantharus tinctus Conrad.
Conus mus Hwass.
Siphonaria pectinata Gmelin.
Arca zebra Swainson.
Barbatia barbata Linné.
Brachidontes exustus Linné.
Lima scabra Born.
Isognomon alatum Gmelin.

2. Shallow water sandy stretches, shallow grassy bays, muddy flats:

Here the sand-burrowing mollusks are at home, and hence we find more pelecypods than in the preceding habitat.

Cerithium variabile C. B. Adams.
Epitonium lamellosum Lamarck.
Sinum perspectivum Say.
Natica canrena Linné.
Busycon contrarium Conrad.
Melongena corona Gmelin.
Oliva sayana Ravenel.
Olivella floralia Duclos.
Marginella apicina Menke.
Conus pealei Green.
Terebra dislocata Say.
Aplysia willcoxi Heilprin.
Cardita floridana Conrad.
Anodontia alba Link.
Lucina floridana Conrad.
Trachycardium egmontianum Shuttleworth.
Dosinia elegans Conrad.

Macrocallista maculata Linné.
Chione cancellata Linné.
Donax variabilis Say.

3. Brackish water estuaries:

This habitat is found all along the shores of the Gulf of Mexico. The mollusks listed here are found both on sandy and muddy bottom as well as on rocky substrata and on objects such as jetties and pilings.

Neritina reclivata Say.
Batillaria minima Gmelin.
Cerithidea scalariformis Say.
Congeria leucophaeata Conrad.
Cyrenoida floridana Dall.

4. Mangrove flats:

A few species are found predominantly in this habitat.

Littorina angulifera Lamarck.
Cypraea zebra Linné.
Isognomon alatum Gmelin.
Ostrea floridensis Sowerby.

CAROLINIAN PROVINCE

This area extends from Cape Hatteras, North Carolina, south to about Cape Canaveral on the east coast of Florida, and from about Tampa Bay on the Florida west coast northward and westward along the shore of the Gulf to about Corpus Christi Bay, Texas. Some elements of this fauna on the western side of the Gulf may go farther south into Mexico, while some tropical forms may reach the vicinity of Matagorda Bay.

The shores of this area have a rather uniform character, without coral reefs or mangrove vegetation. Instead we have mile on mile of sandy beaches, often along low coastal islands, behind which are lagoons, bays, and estuaries with varying degrees of salinity. Frequently we find oyster reefs on the lagoons and bays, but outside of these oyster banks the only solid substrata are mainly in the form of man-made structures such as jetties and pilings.

This province may conveniently be subdivided into the following ecological areas:

1. Outer sandy beaches and nearshore sandy areas:

Epitonium angulatum Say.
Polinices duplicata Say.
Sinum perspectivum Say.
Strombus pugilis alatus Gmelin.
Chicoreus fulvescens Sowerby.
Busycon spiratum plagosum Conrad.
Oliva sayana Ravenel.
Oliva campechiensis Gmelin.
Anadara brasiliana Lamarck.
Noetia ponderosa Say.
Trachycardium muricatum Linné.
Dinocardium robustum Humphrey.
Laevicardium mortoni Conrad.
Dosinia discus Reeve.
Macrocallista nimbosa Humphrey.
Tellina alternata Say.
Tellina versicolor DeKay.
Donax variabilis Say.
Tagelus gibbus Spengler.
Barnea costata Linné.

2. Bays and lagoons, moderate to high salinity, sandy or muddy bottom:

Cerithium variabile C. B. Adams.
Nassarius acuta Say.
Nassarius vibex Say.
Acteocina canaliculata Say.
Pecten gibbus amplicostatus Dall.
Volsella demissus granosissimus Sowerby.
Chione cancellata Linné.
Mercenaria mercenaria Linné.
Abra aequalis Say.
Mulinia lateralis Say.
Ensis minor Dall.

3. Bays and lagoons, brackish water:

Neritina reclivata Say.
Littorina irrorata Say.
Polymesoda carolinensis Bosc.
Rangia cuneata Gray.

4. Jetties and oyster reefs in bays:

Crepidula plana Say.
Thais floridana Conrad.
Anachis obesa C. B. Adams.
Brachidontes recurvus Rafinesque.
Crassostrea virginica Gmelin.

DEEPER WATERS OF THE GULF OF MEXICO

In these deeper waters we find many species that show a relationship with the tropical element of the Caribbean area. We have, for instance, *Terebra taurinum* Humphrey (*flammea* Lamarck) and *Sconsia striata* Lamarck which extend into the West Indies. Others are peculiar to the Gulf. The explorations that are now going on in the Gulf of Mexico and future dredgings will unquestionably bring to light many more new and interesting forms.

Gaza superba Dall. (W)
Murex beaui Fischer and Bernardi. (W)
Oocorys bartschi Rehder. (G)
Fusinus couei Petit. (G)
Scaphella junonia Shaw. (G)
Conus sozoni Bartsch. (G)
Polystira albida Perry. (W)
Polystira tellea Dall. (G)

Terebra taurinum Humphrey. (W)
Anadara baughmani Hertlein. (G)
Aequipecten glyptus Verrill. (C)
Amusium papyraceum Gabb. (W)
Pitar cordata Schwengel. (G)

(W) Also known from the West Indies.
(G) Known only or almost solely from the Gulf of Mexico.
(C) Found also in the Atlantic off the southeastern United States.

In this brief survey of our present-day knowledge of the mollusks of the Gulf of Mexico I have attempted to list some of the conspicuous species found in the various parts of the Gulf and have pointed out how little we actually know of the mollusks. There has lately, however, been an increase in interest in this region, and we can look forward to valuable contributions on this subject in the not too distant future.

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CEPHALOPODA OF THE GULF OF MEXICO[1]

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The taxonomy and biology of the cephalopods of the Gulf of Mexico have been neglected by workers in the field of malacology, and consequently, records and reports are very meager. LeSueur (1821) described the first species from this area when he gave the description of *Onykia carribaea*. De Blainville (1823) described several of the loliginid squids which are now known to occur in these waters, the fact which he failed, however, to record. Howell (1868) described *Loligo hemiptera*, a new squid from the Gulf. This species has since been shown by the author to be synonymous with *Lolliguncula brevis* (Blain.).

Verrill (1882), in his report on the cephalopods of the northeastern coast of the United States, lists five species, only, as occurring in the Gulf of Mexico region: *Sepioteuthis sepioidea* (Blain.), *Loligo gahi* Orbigny, *Lolliguncula brevis* (Blain.), *Sthenoteuthis pteropus* Verrill, and *S. bartrami* (LeSueur). Of these, *L. gahi* Orb., which occurs on the Pacific coast of South America and is not found in this area, has been a cause of much confusion ever since as it has been applied to the arrow squid, *Doryteuthis plei* (Blain.).

From 1882 to 1934 the cephalopods of the Gulf of Mexico were ignored due largely to the lack of specialists in this field. In 1934 Johnson's List of the Marine Mollusca of the Atlantic Coast from Labrador to Texas appeared. In it, Berry (1934), who wrote the cephalopod section, records 64 species within its range of which only 15 species are referred to Florida and the West Indies and only one specifically to the Gulf of Mexico.

Robson (1932) published an account of certain octopods sent him by van Hyning mostly from the Gulf coast of Florida, and this account was followed in 1937 by Adam's report on the *Mercator* collections and the description of a new species from Dry Tortugas, *Octopus mercatoris*, since considered by Pickford (1945) to be synonymous with *O. joubini* Robson.

The first major contribution to the knowledge of the cephalopods of the Gulf of Mexico was made by Pickford (1945) in her study of the littoral octopods of the western Atlantic. Three of the six octopods treated in this study are common to the Gulf of Mexico: *Octopus vulgaris* L., *O. briareus* Robson, and *O. joubini* Robson. The only other published records of Gulf of Mexico cephalopods are a record of *O. burryi* Voss from the upper Gulf and comments upon its distribution by Voss (1950, 1951b). Hedgpeth (1950) records *Loligo brasiliensis* Blain. from the Texas jetties, but this is erroneous, the species involved being *Lolliguncula brevis* (Blain.) which is also recorded in the paper.

Thus it is seen that the cephalopodan fauna of the Gulf of Mexico is comparatively untouched, and to date no survey or monograph upon them has been published such as has appeared for those of other areas such as the Mediterranean Sea or the Hawaiian Islands. According to some zoologists the lack of published records indicates that maybe this area is fairly devoid of specimens. However, an examination of the material, still unreported, from the *Atlantis* circumnavigation of Cuba in 1937–38 presents another picture. The large collection made by that vessel and recently examined by the author contains many new records for the Gulf of Mexico and several species which are new to science. Of the entire collection only a single specimen has been recorded in the literature (Pickford 1946).

Since the initiation by the United States Fish and Wildlife Service of the exploratory fishing by the *Oregon* an entirely new and rich cephalopodan fauna has unfolded in the Gulf of Mexico. The collections made by this vessel are rather large and at this date (September 1952) are in the process of being worked up by the author.

From the material so far examined it appears that there is a strong connection between the

[1] Contribution No. 124 from the Marine Laboratory, University of Miami.

cephalopodan fauna of the Mediterranean Sea and the Gulf of Mexico. The *Oregon* material, both benthic and pelagic, parallels very closely the material from the Mediterranean both in genera and species. Considering the sometimes rather long planktonic life of many of the larval forms and the sweep of the North Equatorial Current into the Caribbean and thence into the Gulf of Mexico, such distribution is not surprising. This close connection is best exemplified by the presence of *Pteroctopus tetracirrhus* (delle Chiaje), apparently quite common in the Gulf of Mexico, which was known previously only from the Mediterranean Sea and a single record from the Azores, and *Scaeurgus unicirrhus* Orbigny, a related genus, which is well known in the Mediterranean but not elsewhere in the Atlantic but was recently reported by Voss (1951a) as occurring along the southeast Florida coast and presumably in the Gulf of Mexico.

Pickford (1946) reported the presence of *Vampyroteuthis infernalis* Chun taken by the *Atlantis* in 1,480 meters from the Gulf of Mexico. This form has not been found in the Mediterranean presumably due to the shallowness of the sill at the Straits of Gibraltar, a factor which does not enter into the discussion of the Gulf of Mexico due to the greater depth of the Yucatán Channel. A discussion of the bathypelagic conditions of this species may be found in the above-mentioned paper.

The extent of the distribution of the Caribbean and Atlantic species into the Gulf of Mexico at the present time is unknown. In the appended list of species known to occur in the Gulf of Mexico those with asterisks have been reported only from the Gulf Stream in the vicinity of Miami or from the Florida Keys. Thus their presence in the Florida Current which sweeps through the southern portion of the Gulf of Mexico must be assumed, yet they have not been reported from the rather extensive hauls made by the *Oregon*. One species investigated by the author, *Sepioteuthis sepioidea* (Blain.), is known from both sides of the Gulf Stream from below its origin in the Lesser Antilles to Bermuda, but there is no record of its occurrence in the Gulf of Mexico proper. The cause of this rather peculiar distribution or limitation is not known.

So little is known concerning the life histories of the cephalopods, especially the octopods, in our area that only generalities can be drawn. From the literature and independent investigations it seems apparent that the octopods and decapods spawn during the spring, although there are indications that some spawning occurs throughout the year. In general, the octopods care for their spawn by brooding over the eggs which are attached either singly or in festoons beneath rocks or in old mollusk shells. Certain of the octopods, particularly those with large eggs (10–15 mm.), hatch out fully developed and immediately take up a benthic life. Others with small eggs hatch out as temporary members of the plankton and spend a certain interval of time, from a few days to several weeks or months, in a drifting state after which they settle to the bottom. The decapods, at least for the few examples known, attach their eggs to the bottom either to rocks, algae, or other objects, and leave them uncared for until hatching whence they become part of the temporary plankton; others attach their eggs to floating objects at or near the surface. Among many exceptions to these are *Vampyroteuthis infernalis* Chun which reportedly has free pelagic eggs and *Argonauta argo* L. in which the minute eggs are retained within the egg case by the female.

The length of life in cephalopods is uncertain and a matter of some dispute. Verrill (1882) suggests that *Loligo pealei* LeSueur reaches maturity in about 2 to 3 years. The actual span of life is uncertain but is believed to average, at least in the smaller species, about 2 to 4 years.

Cephalopods may be either free-swimming open ocean forms such as the Ommastrephidae, benthic such as the Octopodinae, bathypelagic as the Vampyroteuthidae and Spirulidae, or planktonic as in the Cranchiidae. In general, the Loliginidae, a group of great commercial importance in some areas of the world and found in large numbers in the Gulf of Mexico, are free-swimming forms found in coastal waters never far from land. The food of cephalopods consists mainly of crustaceans, bivalve mollusks, and small fish. In return, they furnish a considerable portion of the diet of many fishes. As many as 24 pairs of beaks of *Argonauta argo* L. have been taken by the author from the stomach of a single sailfish (*Istiophorus*). Springer (personal communication) records sucker disc marks the size of a half dollar on the skin of a young sperm whale taken in the Gulf of Mexico, and a single specimen of *Architeuthis* sp. badly

mutilated by sharks was taken from the surface of the Gulf Stream off the Florida Keys. The specimen was measured by the author and estimated to be about 15 feet long when entire so that the presence of the giant squid in these waters is now confirmed.

The number of individual species of cephalopods found in the Gulf of Mexico is rather difficult to determine due to the previously mentioned lack of records. However, the completed results of the *Oregon* explorations will materially increase our present knowledge of this interesting fauna. The following list of species arranged in their taxonomic order includes species which have been taken from the plankton of the Gulf Stream off Miami and as such should be found in the portion of the Florida Current traversing the Gulf of Mexico. Certain others have been reported thus far only from the Lower Florida Keys. Both of these groups are marked with asterisks, and only those not so marked have been actually found in the Gulf of Mexico proper. Many more records could be added from the Caribbean area, but as the presence of these species in the Gulf of Mexico has not been proved they are not included in the present list.

SYSTEMATIC LIST

Order DECAPODA

Family SPIRULIDAE:
Spirula spirula L., 1758.

Family SEPIOLIDAE:
Rossia (*Semirossia*) *tenera* Verrill, 1880.
Rossia (*Semirossia*) *equalis* Voss, 1950.

Family LOLIGINIDAE:
Lolliguncula brevis (Blain.), 1823.
Loligo pealei LeSueur, 1821.
**Sepioteuthis sepioidea* (Blain.), 1823.
Doryteuthis plei (Blain.), 1823.

Family LYCOTEUTHIDAE:
Lycoteuthis diadema (Chun), 1900.

Family ENOPLOTEUTHIDAE:
Abraliopsis morisii (Verany), 1837.
**Thelidioteuthis alessandrinii* (Verany), 1851.
**Pyroteuthis margaritifera* (Rüppell), 1844.
**Pterygioteuthis giardi* Fischer, 1895.

Family ONYCHOTEUTHIDAE:
**Onykia carribaea* LeSueur, 1821.
Onychoteuthis banksii (Leach), 1817.

Family ARCHITEUTHIDAE:
Architeuthis sp.

Family OMMATOSTREPHIDAE:
Illex illecebrosus (LeSueur), 1821.
Sthenoteuthis bartrami (LeSueur), 1821.
Sthenoteuthis pteropus Steenstrup, 1856.

Family CHIROTEUTHIDAE:
Chiroteuthis lacertosa Verrill, 1881.

Family CRANCHIIDAE:
Cranchia scabra Leach, 1817.

Order OCTOPODA:

Family VAMPYROTEUTHIDAE:
Vampyroteuthis infernalis Chun, 1903.

Family STAUROTEUTHIDAE:
Grimpoteuthis umbellata (Fischer), 1883.

Family OPISTHOTEUTHIDAE:
Opisthoteuthis agassizii Verrill, 1883.

Family ARGONAUTIDAE:
**Argonauta argo* L., 1758.
**Argonauta hians* Solander, 1786.

Family TREMOCTOPODIDAE:
**Tremoctopus violaceus* delle Chiaje, 1830.

Family ALLOPOSIDAE:
Alloposus mollis Verrill, 1880.

Family OCTOPODIDAE:
Octopus briareus Robson, 1929.
O. vulgaris L., 1758.
O. joubini Robson, 1929.
O. burryi Voss, 1950.
Pteroctopus tetracirrhus (delle Chiaje), 1830.
**Scaeurgus unicirrhus* Orbigny, 1840.

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SUMMARY OF OUR KNOWLEDGE OF THE OYSTER IN THE GULF OF MEXICO

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The American oyster, *Crassostrea virginica*, in the Gulf of Mexico is characterized perhaps most of all by its versatility in adapting itself to different habitat niches. There are few places where at least a scattered growth of oysters is not found along the 3,600 miles of tidal shore line from Cape Sable in Florida to the Rio Grande in Texas. The distribution of this oyster population is more impressive if we consider its area. There are probably more than 1,400 square miles of water bottoms along the Gulf coast suitable for and more or less populated with oysters. In some areas the oyster communities consist of small isolated patches only a few yards in area which are elevated like islands in a "sea" of too soft mud. Where the bottom is more firm the communities may cover many acres, and reefs up to 25 miles in length are not unknown.

Oysters establish successful colonies in the range from a foot above mean low water to a depth of 30 to 40 feet in some of the deeper channels. Their occurrence is everywhere dependent on a suitable or rather a physically possible substratum. They compete with the tree oyster for space on the mangrove roots; they cover bridge footings and piles of old ballast rock, and have even been found 5 miles out in the open Gulf on an oil well rigging (Gunter 1951a).

In well-protected areas small clusters and single oysters become established on pure sand bottoms. On mud bottoms, too soft to support a reef, single oysters may grow until their own weight carries them below the surface. New spat settle on the edges of such oysters and grow until they, in turn, sink into the mud. Formations such as these with a living oyster attached to buried older generations may extend like poles 3 feet or more into the soft substratum. Oysters persist in isolated marsh ponds whose waters connect with the open sea only for short intervals in time of flood or storm. Scattered individuals attach to the roots of marsh grass fringing the bayous and bays or settle secondarily on mussels growing in the marsh. With natural cultch frequently at a premium oysters are found attached to crabs, turtles, and even on the shell of their worst enemy, the drill.

More typically, reefs build up on the sticky mud bottom found in most of the coastal bays and estuaries along the Gulf shore.[1] The foundations of some of these reefs have persisted since prehistoric times. Successive generations of oysters, attaching to the older oysters and dead shells, have created deposits many feet in thickness. The living population forms an infinitesimal percentage of the total mass on such reefs. In other areas, although the reef may have existed for innumerable years, the substratum of shell is relatively thin, comprising little more bulk than that of the living oysters. In these cases, the high population density of commensals, which excavate the valves, and perhaps chemical factors in the environment lead to the rapid disintegration and disappearance of the old shells.

A fundamental requirement in the ecology of the oyster is the mixture of salt water from the Gulf or ocean with the fresh water from land drainage. The characteristics of the growing oyster community, dependent in large measure on the salinity level resulting from the admixture of these waters, are governed not only by the average salinity levels but also by the extremes of seasonal fluctuation in the total salt content. The size of the population and of the individual oyster, appearance of the shell and quality of the meat, reproductive potential, commensals, predators, parasites, all of these and probably a host of other factors have an obligatory relation to the salinity level of the environment.

[1] The formation of oyster reefs in the Gulf of Mexico is discussed in detail by W. A. Price, p. 491.

The majority of Gulf oyster communities fall into one of four distinctive categories which I classify on the basis of arbitrarily selected average salinity levels. Intergrades between the categories and exceptions to the generalizations are necessarily common, but they do not seriously alter the over-all description. Permanent communities establish themselves and flourish within a salinity range of 10 to 30 parts per thousand. In years of drought or of excessive precipitation populations may appear sporadically in areas normally having salinity levels too low or high to support a population.

Oyster reefs located near the head of a typical estuary comprise the first category. In such regions the salinity ranges annually from 15 parts per thousand to 0 and averages near 10 parts per thousand or below. The sparse population reflects the marginal nature of this environment. Oysters are mostly small and rounded, with smooth, whitish shells. The rate of spatfall is low, and although young oysters grow well their first season, growth of older oysters is relatively slow. Average annual mortality rates are high, and the population is periodically decimated by excessive fresh water in years of flood. Primarily, such reefs are of commercial use as seed areas. In the occasional years of drought these populations may show, however, an excellent growth and yield a good harvest. Typically, these oysters are free from most fouling organisms, and there are few predators or parasites present. These oysters have many characteristics in common with populations growing at or above mean low water regardless of salinity level.

The next definite community type is found where salinity levels fluctuate between 10 and 20 parts per thousand with a yearly average near 15 parts per thousand. The population density of oysters on these reefs reaches a maximum because of high reproductive ability, availability of cultch, and a relatively low concentration of predators. The growth of individual oysters is moderately good and quite uniform so that the population forms rather definite year classes. Oyster valves are usually smooth and dense, although in some areas they may have moderate infections of the boring sponge and clam. The oysters form large or small interlocking clusters, depending on the nature of the bottom. Their narrow shape makes them difficult to handle commercially except as canning stock. When cultivated they yield clusters of two or three better shaped oysters that are suitable for the raw trade. The meats are of high nutritional quality but are frequently insipid to the taste. The increased number of associated animals on these reefs leads to intense competition for both food and space. Barnacles and mussels are frequently present in such numbers as to interfere with oyster culture. While these communities prosper biologically in most years, in times of drought they may experience severe losses due to predation by the drill. In flood years the growth of the population may be retarded for several months.

The third category of oyster reefs is found nearer the mouth of a typical estuary, in areas having an average salinity level of 25 parts per thousand. Annual fluctuations in salt content of water range from a low of 10 to 12 parts per thousand in the spring to about 30 parts per thousand in the dry season. The community here is characterized by unusually good growth, although this factor may be masked by the large amount of shell erosion and predation. The variety of animals living within the oyster community reaches a maximum at this salinity level. The reproductive potential of the oysters probably reaches a maximum here too, but the high population density found in communities at lower salinity levels does not occur here because of the large numbers of parasites and predators. Mortality rates of the very young oysters are relatively high. Having survived its first season the oyster's chances for survival are good. The shells have a massive appearance and may be greatly eroded. The valves show heavy concentric ridges, indicating periods of fast growth rates. These communities are consistent producers of large market oysters of excellent quality. But the environment has its greatest value when used as a bedding ground. Medium-sized seed planted here quickly matures and may be harvested before the usual predators and parasites are established. The decreased spat survival prevents the transplanted oyster from becoming "wrapped up" in young growth. The periodic complete harvesting of these areas when used as bedding grounds prevents or greatly retards the accumulation of undesirable commensals.

The fourth type of oyster community is found at the junction of the typical estuary with the waters of the Gulf where salinity levels are con-

sistently high. Although oysters exist here the environment is just as marginal as in the first category considered. The population is again characterized by its sparseness, slow growth rates, and excessive mortality. The dearth of suitable cultch and the high concentration of predators are important factors in the low survival rate of the spatfall. In most years the commercial importance and the reproductive capacity of reefs in this location are of negligible importance. Following disastrous floods this community, by providing larvae, may be the all-important factor in repopulating the flooded areas where the oysters have been destroyed.

Factors other than salinity levels may exert a profound influence in determining the character of the oyster community. The most important among these are the nature of the bottom, the type of cultch, the amount of water current carrying a supply of food, and the degree of artificial cultivation. It is significant that when young oysters are moved to a new environment they quickly acquire the attributes of the population already present there. It is also of interest to note those instances in which a characteristic type of oyster has acquired a geographical name and becomes well-known in the trade. The practical oysterman may discover that there are other geographic locations which produce essentially the same type of oyster; perhaps we find that 100 boatloads of "name" oysters are annually marketed from a geographic area which can produce only 25 boatloads. This should not be regarded as a case of deception on the part of the producer, for a "name" oyster actually implies a certain quality of product, and similar environments can produce oysters of essentially indistinguishable quality regardless of how far apart they may be geographically.

Very specialized communities exist on wharf pilings, especially in channels having a high current velocity. Isolated marsh ponds may produce characteristic populations. Noteworthy among these is the occasional colony of "Marennes" oysters whose flesh is colored a deep green by the abundance of a particular diatom in its food supply.

Natural oyster reefs are still found occasionally and were quite common at the turn of the century. The only essential difference in their appearance from that of cultivated reefs lies in the fact that, being unharvested, the population builds up until it breaks the water surface. At low tide many oysters are exposed to the atmosphere. Growth along the ridges of these reefs is usually less than that of the population average. The shells are polished and have a reduced number of external and internal commensal organisms. The oysters are scattered in small clusters. There is a coarse substratum consisting primarily of shell fragments. Buried inches deep in the substratum and usually growing quite well, considering the seemingly unorthodox position, there is often a fair number of older oysters. Where depth of water over the reef is greater, the clusters of oysters become larger, and the individual oysters attain a larger average size. Although the oysters are very long, they are correspondingly narrow with deeply concave attached valves and flat or even concave upper valves. Attached to the older oysters may be three or four, perhaps more, younger generations. As a rule, the quality of meat of such oysters is inferior, although the amount of spawn produced by them may be tremendous. The periphery of these reefs is often sharply defined, the outermost fringe of oysters showing luxuriant growth, while a foot beyond lies a muddy ooze too soft to support a single shell.

The interdependence of the myriad of animals associated in this oyster community forms a complex system. In a stable environment their numbers and variety are strictly controlled by the availability of habitat niches even though their food supply is primarily obtained from without. Relatively slight changes in the external environment may drastically alter, however, the entire make-up of the community.

This description of the natural oyster community is probably equally applicable to the oyster community of past ages. The evidence for the antiquity of the oyster in the Gulf is impressive, and the early discovery of their value as food is shown by the Indian shell middens which dot the coast line. Vast deposits of buried shell exist in all of the Gulf States. These banks are usually in 8 to 10 feet of water under a layer of mud of varying thickness. The deposits range from a few inches to 25 feet and more in depth, and no one knows their extent. For the most part the oysters on these old reefs did not grow to any larger size, i. e., live any longer, than oysters do today. The average shell size in many deposits is considerably

less than that found on a modern reef of planted oysters, and we may assume that they did not compare in quality with the cultivated oyster of today.

The enormous quantity of shells in these buried banks does not indicate an unusually high rate of productivity but rather speaks for the untold eons that passed in the formation of such deposits. These old reefs constitute an extremely valuable resource in modern times, since they are composed of relatively pure calcium carbonate (Shearon 1951). The chemical industries of Texas alone, in the decade beginning 1940, consumed more than 45 million tons of these shells. Similar deposits are extensively exploited in Louisiana and to a lesser extent in the other Gulf States. Examination of these reefs reveals striking similarities to the natural communities we find today. Many of the buried shells show light to heavy infestations with boring sponge; some shells are pitted with excavations like those made by the modern boring clam; encrusting bryozoans are present; and of frequent occurrence are the shells of conchs, quite similar if not identical, with the modern *Thais*.

The diversity of habitats existing along the coast of the Gulf causes a parallel diversity in the pattern of growth and reproduction in the oyster so that we may draw a generalized picture of the course of events and indicate the significant exceptions.

In midwinter the gonad tissue of mature oysters is inconspicuous, but by February or March, depending on water temperatures, active gametogenesis takes place. The gonad may form a layer a quarter of an inch or more in thickness by the time spawning commences in early spring, but frequently its thickness is far less. The gonad layer retains much of its original volume throughout the summer; spawning continues regularly until October. Mass spawnings of the population are clearly defined and typically occur several times throughout the summer in a given location (Ingle 1951). This is in contrast to the condition in northern waters where a single mass spawning of major importance usually occurs in early summer.

Oyster larvae are found in the plankton in the period from April through October. It is probable that their free-swimming period is significantly shorter in these waters than along the Atlantic coast because of the sustained higher temperature levels during the summer months. The production of larvae and the resulting spatfall may show peaks of intensity in any one or all of the summer months. At Pensacola the pattern is quite variable from year to year, but during the month of July larval production and spatfall are consistently lower than during the rest of the spawning season. These conditions contrast significantly with those on the Atlantic coast. In Long Island Sound, for example, although there is scattered spawning during the summer period, the majority of spawn is produced in a relatively short time about the end of June (Loosanoff and Engle, 1940). The relative abundance of larvae in the plankton at Pensacola in the period 1949–1951 shows a good correlation with the spatfall in the area, although the quantity present at any one time seems small in comparison with the amount of set produced. In this area there are no commercial reefs; the oyster population is confined to pilings and similar locations out of reach of the conch. In Mississippi Sound, where the oyster reefs are extensive, 50 percent of the volume of plankton samples collected during the height of the spawning season may consist of oyster larvae.

Spat production is heavy but erratic all along the coast; in certain localities spatfall and survival are particularly good. As is true on the Atlantic coast, the areas of best spatfall are frequently areas of relatively poor growth. From the earliest times Louisiana oystermen transplanted seed oysters from setting grounds east of the Mississippi and placed them in areas west of the delta where growth is especially rapid. It is quite possible that the poorer record of spat production in high salinity areas is due to predation rather than to a real decrease in setting rates. In the Pensacola area the cumulative spatfall during a season may be as high as 1,000 spat to the square inch. This intensity of spatfall poses a significant problem to the oyster industry. In areas where oysters set heavily they become so clustered in their growth that they are difficult to handle commercially and have meat of inferior quality.

Competent observers have reported spatfall during other months of the year at widely separated points along the coast, but these instances are exceptions to the general picture of larval

production. The number of spat produced under these circumstances is always quite small. The most reasonable explanation for this situation is that oysters on the mud flats are induced to spawn sporadically in the wintertime because of the sharp elevations in temperature which may take place in small, poorly circulating bodies of water. Water temperatures of 10° to 20° C. in the main bays and estuaries during the winter are not high enough to permit spawning but may permit the growth and setting of the larvae produced in isolated bayous and marsh ponds.

Growth rates of oysters in the Gulf are reputed to be astounding when compared to the rates along the Atlantic coast. This reputation is based on impressions of oystermen, a few fortuitous natural experiments, and a very meager amount of scientific data based on exceptional conditions. It is certain that during its first year the oyster grows to a length of two or more inches on the average. Under special circumstances and under experimental conditions at Pensacola a growth of 3 and 4 inches has been obtained in 12 months. It should be noted that a growth of 2½ inches during the first season is not at all unknown in the Chesapeake area, and July spat have been reported growing to a length of 2¾ inches before their first hibernation period in Virginia (Mackin 1946). Since the growth of oysters in the Gulf is not interrupted by a hibernation period, it would be more surprising if they did not grow up to 3 inches during their first year. In those cases where oysters grow 5 to 6 inches in 24 to 36 months, and there are many such instances, the oysters are usually of the inferior "coon" type. Oysters growing in crowded positions can increase in size only in one direction, and so they soon become unusually long. Oysters growing as "singles" can increase in size in all directions, and single oysters in the Gulf do not exhibit unusual growth rates after their first season (Moore and Pope 1910). Cultivation procedures developed since 1900 by oystermen in Louisiana involve the transplantation of year-old seed to better growing areas and the marketing of the oysters from 18 to 24 or more months later. Good-sized market oysters produced along the Gulf coast probably average three or more years in age. In the Gulf area major increases in growth, measured by length and width, take place in the months of November through March when water temperatures range from 10° to 20° C. The major increases in size in New England oysters take place in the summer months at similar temperature levels (Loosanoff and Nomejko 1949).

The time required for a Gulf oyster to reach sexual maturity is significantly shorter than in northern waters (Menzel 1951). Approximately one-third of the oysters setting in the early part of the summer become sexually mature by the time they are a month old and still less than an inch in diameter. It is probable that a majority of the spat attain sexual maturity during their first season and make a significant contribution to the larval population of late summer. In other words, it is a normal event for two generations of oysters to be produced in this area each summer.

During the past century there have been many changes of a temporary or permanent nature in the continuity of oyster communities and in the physical location of the reefs. Man has caused or accelerated many of these changes. Other changes due to the natural succession of events in an estuarine environment are presumably of no greater importance today than they were in prehistoric times.

The many rivers draining into the Gulf annually deposit an enormous load of silt which produces multiple effects in the estuary. The major silt load deposited in the delta gradually pushes the head of fresh water seaward. In the past 50 years the Colorado River has filled in more than 6,000 acres of upper Matagorda Bay, and delta mud now lies on top of once productive oyster reefs (Baughman 1947, unpublished ms.). In its progress to the sea the water carries much silt with it, and this has additional effects on the oyster population. It decreases the penetration of sunlight into the water, thus limiting the production of plankton, the oyster's food supply. Fine silt, by coating the old shells on the bottom, makes them no longer available as cultch for the young oysters (Butler 1951).

An entirely different type of change has been brought about by man in the oyster areas west of the Mississippi River. In this region a number of bayous in the past contributed a regular supply of fresh water to the bays and inlets along the coast. Man has channeled these bayous and changed their exits to the sea so that they contribute

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fresh water to the area only in times of flood. As a result of these changes in the drainage system the inner bays and lakes lying some distance from the coast, formerly entirely fresh, have now become saline enough to support large populations of oysters. Connecting bays lying between them and the Gulf have, in turn, become more salty The increased salt content here encouraged the survival of the conch which has decimated or destroyed entirely many large reefs (Moore and Pope 1910). A secondary result from this channeling has been an increase in erosion along the shore. The annual load of silt brought down by the rivers or bayous no longer reaches the coastal areas, where in the past it counter-balanced shore erosion and created a fairly stable coast line. Shore erosion, now uncompensated, has destroyed some of the barrier reefs; formerly protected bays are now open to the Gulf and cannot support oyster populations. Conversely, some bays which formerly had connecting channels to the Gulf have become landlocked by sand spits, and their oyster communities have largely disappeared. There probably has been no great net change in the amount of bottom available for oyster culture, but the reefs have migrated inland away from the sea and have become more susceptible to the effects of seasonal floods in their new location. There are some places along the coast where man has opened up channels and deposited spoil banks in the construction of inland waterways. These operations have frequently changed salinity levels permitting an increased survival of oyster predators and, in some cases, have buried reefs in mud.

Extensive changes in oyster communities have also resulted from harvesting methods. Redfish Reef in Galveston Bay, which was more than 5 miles in length, produced a large annual harvest throughout the nineteenth century. In 1890, by the use of a tug and two power dredges, this reef was eradicated in a single year (Baughman 1947, unpublished ms.). Overharvesting without replacement of shell cultch inevitably causes the deterioration of a reef. In places where overharvesting has continued until the dead shells supporting the reef as well as the live oysters have been removed, it has been a matter of but a few years before the area deteriorated to such an extent that even nature could not rehabilitate it.

Oyster reefs are normally established in positions protected during average storm conditions. The occasional hurricanes experienced in the Gulf area may destroy large numbers of oysters in shallow water areas and on sandy bottoms. In 1947, for example, many miles of reef along the north edge of Mississippi Sound were covered with mud by wave action and destroyed (Engle 1948). This area has shown no significant natural rehabilitation in the past 5 years.

We have mentioned some of the factors which may permanently eradicate the oyster reef. There are other items which are of greater or lesser importance in affecting the continuity of the populations.

Crevasses.—Disastrous but relatively temporary changes result from exceptional floods from the river basins. In 1890 the flood of the Nita crevasse extended east from the Mississippi River and affected oyster reefs 180 miles away in Mississippi Sound. Forty miles of oyster reefs lying between Lake Borgne and Biloxi were seriously damaged at that time. The history of floods of the lower Mississippi River shows that, although they may wipe out huge oyster populations in a short time, these populations are quickly reestablished, often at a more luxuriant level than prior to the crevasse. The annual spring floods occurring in most river basins cause some mortality in the oyster population by lowering the salinity of the water, but in most years these losses are insignificant.

Temperature.—The oyster is extremely versatile in adapting itself to changes in temperature and is commonly found where the annual range is from $-2°$ to $+30°$ C. The Gulf oyster is less accustomed to severe cold weather than its Atlantic coast relatives, and occasionally large numbers of oysters growing at mean low-water level are destroyed during sudden winter freezes.

Pollution.—Pollution has constituted a serious factor in the continuity of oyster populations during the past 50 years, but due to more effective control measures, it is becoming of less importance. Oysters have been destroyed in several areas by the effluent from paper mills, for example, and other industrial wastes are reputed to have damaged large oyster-growing areas. The control of industrial wastes no longer constitutes an unsolvable problem. Pollution resulting from

domestic sewage [2] is of great importance, not as it affects the survival of oysters, but as it affects their food value to man. On the west coast of Florida alone, more than a dozen shellfish-producing areas have been closed to harvesting as a health measure (Vathis 1950). To some extent all of the Gulf States are faced with this problem. Actually, the closing of polluted areas to harvesting constitutes a conservation measure as far as the continuity of the oyster population is concerned, but it results in a deplorable waste of a valuable food resource since satisfactory control measures are known.

Disease.—The oyster is undoubtedly afflicted with a large number of diseases, but their effects upon the animal are, for the most part, imperfectly known. The recent demonstration of the infection by the fungus *Dermocystidium marinum* is a significant contribution to our knowledge of the pathology of the oyster in the Gulf. The harmful effects of this parasite are greatest at high temperatures and high salinity levels (Mackin 1951).

Some specific parasite may be the causative agent of the disastrous mortalities which occur among transplanted oysters in some areas of Louisiana during the hot summer months. These mortalities, ranging from 35 to 95 percent of the population in different areas, were unreported 20 years ago. Their frequent occurrence since that time has necessitated entirely different cultural techniques. Now, oysters for rebedding purposes in these areas must be large enough so that a few months' growth will make them suitable for marketing. In the past it was the practice to bed much smaller seed oysters and let them grow for 18 months or longer before harvesting (McConnell 1950).

Oysters are widely subject to infestation with the sporozoan parasite *Nematopsis*. There is no evidence, however, that this micro-organism debilitates or is the cause of mortalities in the oyster (Landau and Galtsoff 1951). Of less common occurrence is the digenetic trematode, *Bucephalus*, whose larvae develop in and cause the deterioration of the oyster gonad. Several other unspecified diseases, as well as infections with bacteria, have been reported recently for oysters in Barataria Bay (Mackin 1951). It is probable that none of these diseases greatly affects the reproductive potential of the oyster community.

Predators.—Man has been the most serious threat to the continuity of oyster populations because of his wanton methods of overharvesting. Overharvesting in the past has taken the form not only of removing all the oysters from the reef but also of removing the underlying cultch which made the reef possible. Reefs so destroyed do not rehabilitate themselves naturally, and the cost of replacing the foundations is not feasible economically. Fortunately, our increased awareness of this problem during the past 50 years has reduced the threat of overharvesting except in isolated areas.

The most serious natural predator of oyster populations in the Gulf area is the conch or oyster drill, *Thais*. The two forms of this species have slightly different appearances; *Thais f. floridana* occurs mostly east of the Mississippi River and *Thais f. haysae*, primarily west of the river (St. Amant 1938). Depredations due to this conch are incalculable. In the Pensacola area and in the southern reaches of Barataria Bay, for example, it makes oyster culture impossible. The snail is distributed wherever oysters are found at salinity levels averaging above 15 parts per thousand. Its populations are periodically decimated in times of flood and show enormous increases in times of drought. The snail reproduces during the summer months simultaneously with the oyster. Large individuals may deposit a half million eggs which develop into free-swimming larvae. After a plankton stage of unknown duration the young snails settle to the bottom and commence feeding on oysters and other sedentary forms. Snails a millimeter in length and a week old can be found actively drilling oyster spat of the same size and age. Large snails have been observed by the author eating spat at the rate of four per hour under experimental conditions. The snails are known to live for at least 3 years and possibly many more under normal circumstances. Its voracious feeding habits, high reproductive capacity, and the fact that its larvae are distributed by water currents combine to make this snail the most destructive oyster predator in the Gulf environment. A few other gastropods present, such as the moon snail, *Polynices*,

[2] A detailed account of pollution in Gulf water is given in the last chapter of this book, pp. 555–575.

may feed on oysters to a limited extent, but their relative importance has not been studied.

The Gulf area is fortunate in not having to contend with the starfish which constitutes so serious a predation problem along the Atlantic seaboard. The black sea drum, *Pogonias*, is described frequently in the literature as a serious pest in the Gulf area (Moore 1907). This writer has no first-hand experience with its activities, but oystermen report it as a nocturnal visitor to areas containing newly bedded oysters. Large schools of fish may destroy thousands of bushels of oysters in a short time. Apparently this fish does not attack the natural oyster reefs.

Various species of crabs constitute a serious but imperfectly defined menace to the oyster population. The blue crab, *Callinectes*, is a common inhabitant of the oyster reef, and there are many observations of its activities in cracking open the soft new growth on oyster shells and eating the meats. In limited areas the stone crab, *Menippe*, is an occasional marauder. Its massive claws are able to crack open oyster shells with ease. Mud crabs of the family Xanthidae inhabit the oyster community in large numbers and undoubtedly consume many of the tiny spat. The list of predators includes the oyster "leech," *Stylochus inimicus*,[2] and other polyclad flatworms of several species which are common associates in the oyster community. These worms may cause serious damage, but evidence indicates that they are secondary rather than primary predators (Pearse and Wharton, 1938). They cause the greatest harm in areas where oysters are already in a weakened condition because of some other factor. In the healthy oyster community they are probably of little importance except in their role as scavengers.

Commensals.—Three commensal animals occur in numbers sufficient to affect the biology of the oyster seriously. However, their injurious effects are of greater importance to the oyster industry than to the continuity of the species. The boring sponge, *Cliona*, the boring clam, *Martesia*, and the blister worm, *Polydora*, dwell within the oyster shell, existing at various population densities depending upon the environment. The sponge and clam are more prevalent in areas of high salinity. The annelid is more commonly associated with soft, muddy bottoms extending into areas having lower salinity levels. All of these animals compete with the oyster for food. Their injury to the oyster is difficult to evaluate, but obviously they force it to secrete excess amounts of shell in order to keep the burrows of these organisms separated from the oyster meats. Both the sponge and clam form extensive excavations opening on the exterior surfaces of the shells, making the shells friable and hard to handle commercially. Such oysters usually have a massive eroded appearance, and typically, the meats are of inferior quality. The annelid lives on the internal surface of the valve where it is sealed off in a blister by the oyster. Its injurious effect is primarily a decrease in the esthetic appeal of oysters on the half shell, although in areas outside of the Gulf unusually large colonies of these worms have suffocated oyster communities.

The commensal crab, *Pinnotheres*, of frequent occurrence in oysters in high salinity areas along the Atlantic coast where it may be occasionally injurious, is uncommon in the Gulf. A related species, however, is often present in the bay scallop in Florida waters.

The animals and plants associated with the oyster community are legion. Some have importance in competing with the oyster for attachment surface, and some in competing for food. Their biological and economic importance to the oyster population are mostly a matter of conjecture. The relative abundance of the commensal forms varies greatly from one oyster reef to another. In low salinity areas these forms are relatively rare, but their numbers increase to species climax at different higher salinity levels. The following listing of the more common members of the community does not indicate their relative numbers or importance; any one of them at some time or place may completely envelop the oysters, decreasing the available food supply and preventing the attachment of oyster spawn:

Algae, of various types.
Sponges, both encrusting and boring.
Hydroids and anemones.
Polychaete worms.
Other mollusks, including *Anomia*, *Crepidula*, *Ostrea*, and *Mytilus*.
Barnacles.
Bryozoa, both encrusting and upright.
Tunicates.

[2] *Stylochus frontalis* Verrill according to L. H. Hyman. See page 301 of this book.

In discussing the competition among sedentary organisms for space on the oyster reef it is important to note that in some areas the oyster is its own worst enemy. Huge numbers of spat settle in areas large enough to support only one or perhaps two adult oysters. Obviously, in the struggle for existence, the faster growing spat soon overrun and smother their neighbors. Where available cultch is limited, spat mortality may be enormous.

At the turn of the century the United States Bureau of Fisheries made notable contributions to our knowledge of oyster biology in the Gulf by conducting extensive surveys at the request of the several States. As a direct result of these studies, conservation laws were enacted in Louisiana which greatly stimulated the oyster industry. Oyster cultivation practices were improved, and production increased significantly (Seferovich 1938). Oystermen of that State made a regular practice of obtaining seed oysters from reefs in low salinity areas east of the Mississippi River and replanting or bedding them west of the river in bays where salinity levels were higher and the environment fostered rapid growth. Such oysters became suitable for the market in 18 or more months.

In the past 15 years this culture method has changed radically because of high summer mortalities. As a result, the seed which are now bedded are actually market oysters, and they are relaid for only a few months before harvesting. Today, Louisiana is foremost among the Gulf States in conducting an active shelling and seed planting program, but other States are becoming increasingly active in this regard. It is significant that in Texas, where the least has been done in providing cultch for spat, the industry has seen its greatest decline.

Although the oyster has greatly decreased in many sections of our Atlantic coast line because of man's activities, it is improbable that the immense oyster population of the Gulf could be eradicated. However, there are many once productive areas in which the industry is now nonexistent because of over harvesting and lack of cultivation. The industry faces many problems in the Gulf area. A majority of them could be resolved by the application of well-known and tested cultivation techniques by the enactment of sound conservation measures based on established data and by the enactment of legislation which would stimulate production as well as protect the private planter.

One of the unsolved problems in the Gulf area is a method for economically controlling predation by the conch. When these methods are discovered, large and valuable areas that are now useless can be cultivated. Another and rather curious problem exists because of the unusually intense spatfall in many regions. On the North Atlantic coast the first problem of the industry is to procure sufficient seed oysters for cultural purposes, while along the Gulf coast the problem is to dispose of the superabundance of seed. The too heavy spatfall produces badly clustered, misshapen oysters; oysters that are almost impossible to separate for market purposes without killing more than are saved. Oysters growing in this manner rarely yield a select product. It will be necessary to devise new cultural techniques to utilize this tremendous spatfall. These methods must permit the attachment of only two or three oysters to a piece of cultch and still supply enough cultch so that the vast numbers of spat present are not lost to the industry.

An economic problem of perhaps greater importance is a need for the controlled use of mechanized equipment in cultivating and harvesting the crop. The short supply of labor is a significant factor in the lowered production of the industry. Hand methods are largely retained because their inefficiency constitutes, in a negative way, a conservation measure. But oystering with hand methods is hard work and good cultivation requires nearly year-round attention. As a result, the labor pool is largely claimed by the shrimp industry which offers high returns for a relatively short season. The question of using tongs or power dredges on the reefs is a recurrent argument.

It is not irrelevant to consider, on a theoretical basis, just what the Gulf oyster industry could produce in terms of food for man. Scientific plantings made in Louisiana 50 years ago, the experience of planters in that State since then, and recent work done in Florida, all provide parallel figures on which to base our estimate. An acre of good oyster bottom, properly handled, can produce 900 bushels per year under exceptionally good circumstances, and in commercial practice a yield of 500 bushels can be obtained. For this estimate I have arbitrarily selected a

figure of 300 bushels per acre per annum. A bushel of Gulf oysters will yield 4 pounds of completely drained meat. When we assume that at least 1,400 square miles of Gulf oyster bottoms could be put into production, we find that on a sustained yield basis the industry could produce in excess of 500,000 tons of oyster-meat each year. The entire production of the United States now approximates less than 10 percent of this figure.

There are at least three other species of oysters in the Gulf, all members of the genus *Ostrea* (Gunter 1951b). *O. equestris* is a small species occurring discontinuously from Texas to Florida. *O. frons* has been reported most frequently from southern Florida, but it exists at Pensacola and has been found off the Texas coast. These two are quite similar; they exist at salinity levels usually above 25 parts per thousand and are most commonly found at the junction of Gulf and bay waters. Their setting periods coincide with the spatfall of *C. virginica*. In areas where one of these species occurs with *C. virginica* they may be confused because of their superficial similarity when about an inch in diameter. Large numbers of *O. equestris* were actually transplanted in Apalachicola Bay at one time on the mistaken assumption that they were seed of the commercial oyster. In the fall months *C. virginica* spat quickly surpass the spat of *Ostrea* in length. At the age of 1 year, *O. frons* and *equestris* still approximate one inch in both length and width, although rarely they attain a length of 2½ inches in an unusually favorable environment. Internally, both *O. frons* and *equestris* are distinguished from *C. virginica* by a variable number of denticles on the anterior edges of the valves and by the absence of pigment in the muscle attachment area. These oysters are larviparous, and during the summer months the mantle cavity frequently contains large numbers of offspring in a manner similar to the European oyster, *O. edulis*. Spat of the three oysters, *O. frons*, *O. equestris*, and *C. virginica* were found in abundance on the same cultch at Pensacola during the summers of 1949 and 1950. This mutual occurrence of the three species in time and space is probably infrequent. A third species, *O. permollis*, the sponge oyster, is rather common on the Florida coast in shallow water. It is a small, flat oyster, up to 2 inches in length, yellow brown in color and most frequently found living inside of masses of the bread sponge.

The ecology of the oyster in the Gulf of Mexico parallels, in many respects, conditions found along the Atlantic seaboard. Where significant biological differences exist between the two areas, they are due primarily to the higher temperature levels of the Gulf environment. The biological and economic problems facing the industry here have their counterpart in other oyster producing areas. The industry in the South can include among its distinctive advantages an unlimited area for the expansion of cultivated grounds and a seemingly inexhaustible supply of seed oysters.

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OYSTER REEFS OF THE GULF OF MEXICO[1]

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Caswell Grave (1901, 1905) showed that linear, ridge-shaped reefs of the common edible estuarine oyster now known as *Crassostrea virginica* develop from shell clusters at the more favorable shoreline or near-shore positions, growing out into a passing current and elongate at right angles to it, then branch or curve as the current is deflected by reef extension. This process seems to be valid for the reefs found in the bordering areas of many bays and estuaries. Another class of reefs, elongated parallel with median channels, does not follow Grave's process of terminal growth into a current from its flank but forms along a channel and elongates parallel with the dominant currents of the channel. Paired reefs of this type are found in many inner water bodies, as in central San Antonio Bay, Texas, and the lower James River, Virginia. The reefs of Atlantic estuarine rivers seem usually to be merely elevated ridges on large, oval to quadrate oyster beds. Those of the Gulf coast are not characteristically surrounded by thickly occupied oyster bottoms except along their immediate flanks.

Besides the linear ridge-shaped reefs, many short ridges, or rounded to oval forms are charted, locally called tow-heads.

Mudshell dredgers report that some reefs have a total depth of some 18 feet or more, in places with an interbedded layer or two of mud. Many reefs of Texas bays reach lengths of 1 or 2 miles, a few being 4 to 5 miles long. The longest reef complexes known are the two that curve broadly across the wide mouth of Atchafalaya Bay, Louisiana. The outer, more recently active reef complex is 25 miles long with many narrow channels through it. The older is dead and buried by several feet of sediment.

The known oyster reefs of most regions occur in the inner bays and estuaries in waters neither too exposed to heavy wave action nor too fresh from incoming alluvium-laden river waters. They seem to form chiefly on the more stable bottom areas. Along parts of the northwestern coast of peninsular Florida (28°15′–30°04′ N. Lat.), off the mouth of Atchafalaya Bay, Louisiana, and on the south and west shores of Marsh Island just west of the bay, reefs of *Crassostrea virginica* occur in the Gulf of Mexico within 5 or 6 miles from shore. Here, the Gulf waters are locally diluted to the necessary brackishness.

Several of the small reefs off Atchafalaya Bay have live oysters. Here a large flow of fresh water from the Mississippi enters the Gulf through its largest distributary, the Atchafalaya River. Off the northwestern coast of Florida compact limestones form the floor of the shallowly submerged continental shelf. The peninsula has a widespread artesian water body fed by surface waters entering through the extensively fissured limestones and the many sink holes of the karst topography. Numerous up-welling springs are reported in the stream mouths along this coast, and a few have been reported in the Gulf. The very broad, shallow, gently-sloping continental shelf protects the near-shore waters from breakers and surf, producing conditions in the Gulf similar to a lagoonal environment. The oyster reefs occur in these quiet waters of lowered salinity. They are distributed near shore where the artesian groundwater maps show the 10-foot contour on the piezometric surface to be at the shoreline. These Gulf reefs include forms that project out from a shoreline and also broadly curved and offset forms that are roughly parallel to the coast. Groups of the latter have jumbled patterns of occurrence.

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CHAPTER XVI
TUNICATES AND LANCELETS

THE TUNICATA OF THE GULF OF MEXICO

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The Tunicata or Urochorda are a widely distributed group of exclusively marine invertebrate animals mostly of small but not microscopic size, many being less than an inch and few exceeding 3 or 4 inches in their maximum dimensions. There are probably less than 900 valid species. Evidently they are the survivors of what was a much larger and more important group in past geological times, although, as they are soft-bodied creatures without a shell or hard skeletal parts, they have not left recognizable fossils.

Though of very minor economic importance they are of great scientific interest, as of all the invertebrates they show the closest relation to the vertebrates and are included with them in the phylum Chordata to which the higher animals, including man, belong. In modern classifications they are given the rank of a subphylum of the Chordata.

They are, however, a group that has undergone retrograde instead of progressive evolution. Though the adult tunicates are creatures with a rather low and simple type of organization so that the older zoologists considered them to be shellless mollusks, yet in their larval stage they have so much resemblance (except for much smaller size) to the tadpoles of the amphibians (frogs and salamanders) in certain important structural characters that we cannot dismiss it as mere coincidence and must regard it as indicating common ancestry at some time in the remote past.

Three classes are included in the Tunicata, two of which, the Thaliacea and Larvacea, are free-swimming pelagic forms and are few in species. The third, the Ascidiacea (ascidians), is much the largest and best known class and will be considered first.

The ascidians are, except a few that embed themselves in the sand or mud of the sea bottom, permanently attached animals when adult and depend for food on the minute organisms that the tides and currents bring to them. Their sac-like body of oval or more or less irregular shape is enclosed in a thick outer tunic called the test, which is sometimes gelatinous but more often of tough, leathery consistency.

In it there are only two openings to the outside, both of which are often extended into short tubes. One of the tubes serves as the mouth for the entrance of water for respiration and also brings in their food. The other is the excurrent aperture for the discharge of the water, the waste matter, and usually the eggs or larvae. All ascidians reproduce sexually by means of eggs and spermatozoa, but very many of them, especially those in which the individuals are of quite small size, also reproduce asexually by budding. The new individuals thus formed remain attached to and enclosed with the parent in a common mass of test so that what is termed a colony of many united individuals is formed. Such species are called compound ascidians; the small members that compose the colony, the zooids. Species that do not bud are distinguished as simple ascidians. Compound ascidians may be recognized by the many small apertures belonging to the numerous zooids and often have much superficial likeness to the sponges in association with which they very often grow.

ASCIDIAN FAUNA OF THE GULF OF MEXICO

As far as the ascidians are concerned the Gulf of Mexico is not a distinct faunal region but a part of that which is commonly called the West Indian region, though actually much larger, including all the eastern American tropical and subtropical waters from the Carolinas on the north, with an outpost at Bermuda, to far south on the coast of Brazil. Throughout this vast region there is considerable uniformity as far as many of the commoner species are concerned, and even rare and locally distributed species may appear in

widely separated places within it. In contrast to what is the case with the ascidians of the cold regions of the world, the ascidians of this area are generally found numerous in the shallow waters along the shores and in depths of not more than 5 to 20 fathoms and only rather exceptionally in more than 50 fathoms. In fact, only one species that can be called a really deep-water species (*Pyura antillarum*, obtained near the Lesser Antilles in 496 fathoms) is known from the West Indian region.

Leaving out of consideration a few uncertain forms and a few that are probably better regarded as merely subspecies, only about 81 apparently valid species of ascidians are known from the West Indian region, in the broad sense of that term explained above, which includes all the tropical and semitropical waters of the eastern or Atlantic side of the American continent. Of these, 64 are compound ascidians; the remaining 17 are simple ascidians.

It is remarkable that no less than 71 of these species have already been found in the Gulf of Mexico; 3 of them and 1 additional form as yet undescribed have not been found anywhere else, though future collecting will probably show their distribution to be wider. It is very evident that it is the shallow region that borders the eastern side of the Gulf along the west coast of Florida, and particularly the southern end of it, that has the richest ascidian fauna. Unquestionably, the maintenance, for many years, of the Marine Laboratory of the Carnegie Institution on the Dry Tortugas and the consequent, exceptionally thorough collecting that has been done in that vicinity has contributed much to give us a better knowledge of its fauna, yet that region, with its many shoals and coral reefs, its numerous small islands, and the currents that converge toward the Florida Straits to form the Gulf Stream, provides particularly favorable conditions for such animals as the ascidians; an environment better than we have yet found anywhere else in that region of the world.

In the northern part of the Gulf, ascidians are less numerous in species, though they may be abundant in individuals, except where the water is of reduced salinity near the mouths of rivers, a condition to which most ascidians are very sensitive. There are two northern species (*Molgula manhattensis* and *Bostrichobranchus pilularis*), well-known on the coasts of the Middle States, that occur on the Louisiana coast but have not been found in southern Florida. Possibly this interrupted distribution may be due to the comparatively recent elevation of southern Florida above the sea level.

There are still long stretches of the coasts of the Gulf, including most of the Texan and Mexican parts, that have been very little or not at all investigated, though we can scarcely expect that much that is new will be found there. No ascidians have been recorded from the deep, central part of the Gulf.

Among the commoner and conspicuous ascidians of the Gulf are: Compound ascidians: *Amaroucium stellatum*, *A. constellatum*, *Polyclinum constellatum*, *Didemnum candidum*, *Eudistoma capsulatum*, *E. tarponense*, *Clavelina picta*, *C. gigantea*, *Distaplia bermudensis*, *Perophora viridis*, *Ecteinascidia turbinata*, *Botryllus schlosseri*, *B. planus*, *Botrylloides nigrum*. Simple ascidians: *Ascidia nigra*, *A. interrupta*, *Polycarpa obtecta*, *Styela partita*, *S. plicata*, *Pyura vittata*, *Microcosmus exasperatus*, *Molgula occidentalis*. For descriptions and illustrations see Van Name 1930, 1945.

None of the ascidians or other tunicates of the Gulf appear to have any economic importance, though when small and young they furnish some food for crabs, fishes, and other animals, but the larger ascidians, whether simple or compound, do not seem to be attractive to such predators, owing chiefly to the toughness or unpalatability of the test which forms so much of the bulk of the body or to its lack of enough food value to make it worth eating. None of the Gulf species are used as an article of human diet as a few large species are in some foreign countries. Neither are they known to be harmful, though they sometimes are a component of the growth that fouls the bottoms of vessels, but rarely to any important extent.

THE PELAGIC TUNICATA

These require only brief mention in the present work. Those of one class (Larvacea) are too small to attract notice. One of them (*Oikopleura tortugensis*) was described from and reported abundant near the Dry Tortugas (Brooks and Kellner 1908).

Those of the other class (Thaliacea) are larger and much better known, especially the salpas

which formed the genus *Salpa* in old classifications but are now commonly divided into several genera or subgenera. They are transparent jelly-like creatures of more or less ovate form, having transverse muscle bands which contract and enable them to swim slowly. They are found in the open sea as well as along the coasts. Some of them appear at intervals in immense swarms. The salpas afford a striking instance of alternation of generations; one of solitary individuals alternates with one of aggregated individuals budded off in a chain in which they may remain connected together for a time. Because of the watery, unsubstantial character of their tissues, including the test, they are of small value as food for other animals.

Among the species found in the Gulf of Mexico are: *Salpa* (*Thalia*) *democratica*, a small but often abundant species, *S.* (*Pegea*) *confoederata*, *S.* (*Salpa*) *cylindrica*, *S.* (*Salpa*) *fusiformis*, *Cyclosalpa floridana*. See Metcalf 1918.

Another pelagic genus occurs in the Gulf, *Pyrosoma*, a compound form in some respects intermediate between the Ascidiacea and the Thaliacea and sometimes included in the former group. It forms gelatinous tubular colonies closed at one end which are very luminous at night. See Metcalf and Hopkins 1919.

No monograph dealing exclusively with the Tunicata of the Gulf of Mexico has ever been published. The information about them is widely scattered, much of it in works dealing chiefly with those of other regions or mainly with animals of other groups, often in foreign language or in back volumes of scientific periodicals that few libraries have available. Most tunicates are animals of wide distribution; many occur in both the Old and New World and were originally described in European works, and the insufficient descriptions and obsolete nomenclature used in the older books will often be a cause of confusion. However, a nearly complete bibliography of the systematic literature on the American ascidians, including those of the Gulf of Mexico, will be found in the work by Van Name (1945) listed below. Since that date little of importance has (1950) been published.

The following works will probably be found the most useful to consult for recent information on the Gulf of Mexico Tunicata and references to other literature on them. Several important general works are also listed.

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THE LANCELETS

BRANCHIOSTOMIDAE

By JOEL W. HEDGPETH, *Scripps Institution of Oceanography, University of California*

There are a number of sporadic records for Amphioxus along the Gulf coast indicating the occurrence of one or more species of lancelets throughout the area in favorable localities. According to Bigelow and Farfante (1948) the species occurring on the coast of western and northwestern Florida (as far as Pensacola), sometimes in very large numbers, is *Branchiostoma caribaeum* Sundevall. These authors consider *Branchiostoma floridae* Hubbs (1922), to which specimens from this area were previously assigned, a synonym of *B. caribaeum* and give the range of this species as from Chesapeake Bay to the West Indies. A small collection of lancelets made by T. E. Pulley in Lydia Ann Channel, Aransas Bay, Texas, was determined by Gunter as *Branchiostoma caribaeum* (Gunter and Knapp, 1951). Recently, lancelets have been collected from the Chandeleur Islands and from various places on the Mississippi coast but have not been positively identified (Hefley and Shoemaker 1952).

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CHAPTER XVII
FISHES AND SEA TURTLES

THE ORIGIN, RELATIONSHIPS, AND GEOGRAPHICAL DISTRIBUTION OF THE MARINE FISHES OF THE GULF OF MEXICO[1]

By Luis Rene Rivas, *University of Miami*

The Gulf of Mexico is the northwesternmost of the three Middle American basins. It is a typical, basin-shaped mediterranean sea with an area of 615,000 square miles and a maximum depth of about 2,000 fathoms (Sigsbee Deep) at its center. Its longest axis, oriented SW–NE between Veracruz, Mexico, and Apalachee Bay, Florida, measures about 960 nautical miles, and its short axis, oriented N–S between the Mississippi Delta and the Peninsula of Yucatán, measures about 460 nautical miles. The Gulf of Mexico is separated from the Atlantic Ocean by the Straits of Florida, about 110 nautical miles wide between Cape Sable, Florida, and Cabo Hicacos, Cuba, with a maximum depth of about 900 fathoms (average depth about 500 fathoms). It is separated from the northwestern Caribbean Basin by the Yucatán Channel, about 110 nautical miles wide between Cabo Catoche, Yucatán, and Cabo San Antonio, Cuba, with a maximum depth of about 1,000 fathoms (average depth about 700 fathoms). The total perimeter of the Gulf of Mexico comprises about 3,000 nautical miles of which only about 220 (7 percent) are taken up by the openings (Straits of Florida and Yucatán Channel).

The above conditions would seem to indicate that the Gulf of Mexico contains a characteristic fish fauna of its own appreciably distinct from that of neighboring areas. In this respect, however, it is to a great extent a continuation of the Caribbean region. (See Rivas, 1949, for list of game and commercial fishes.)

There is a very slight amount of subspecific distinction between the fish faunas of the Gulf of Mexico and the Caribbean Sea, and a temperate Atlantic element is present in the Gulf but absent in the Caribbean region. On the other hand, there are several species which occur in the Caribbean region but not in the Gulf of Mexico, and there is no marked transition between the fish faunas of the Gulf of Mexico and the Caribbean Sea or the Atlantic Ocean through the Yucatán Channel and the Straits of Florida, respectively. There is relatively little known of the deep-sea fish fauna of the Gulf, but the present depth of the Yucatán Channel and the Straits of Florida cannot be construed as barriers preventing the dispersal of deep-sea fishes to and from the Gulf. According to the paleogeographic evidence (Schuchert 1935) there was a land barrier across the Yucatán Channel during the Mio-Pliocene, and the Straits of Florida were then shallower than at present. These conditions, however, were relatively short-lived, and their former existence is now reflected in the slight subspecific transition (affecting only very few species) observed through the Yucatán Channel and the presence or absence of certain forms north and south of this strait. The Gulf Stream, entering from the Caribbean Sea through the Yucatán Channel and leaving through the Straits of Florida, is one of the most important factors in making the fish fauna of the Gulf of Mexico homogeneous with that of the rest of the Caribbean area.

Among many others, the genera *Harengula* (Clupeidae), *Mugil* (Mugilidae), and *Centropomus* (Centropomidae) will serve to illustrate the above distributional pattern. Of the three species of *Harengula* (sardines) known from the Caribbean area only *H. pensacolae* occurs throughout the entire perimeter of the Gulf, being rather scarce in the Caribbean Sea. On the other hand, *H. humeralis* and *H. clupeola* are very abundant in the Caribbean Sea but penetrate into the Gulf only as far as the north coast of Yucatán, western Cuba, and southern Florida. *Mugil cephalus* and *M. curema* are the only mullets occurring throughout the entire perimeter of the Gulf of Mexico, whereas, *M. trichodon* penetrates only to the north coast of Yucatán, northwestern Cuba, and

[1] Contribution No. 107 from the Marine Laboratory, University of Miami.

south Florida. *Mugil liza* (*M. brasiliensis* of authors) penetrates to the north coast of Yucatán and northwestern Cuba, but so far it has not been recorded from Florida. *Centropomus undecimalis* (snook) occurs throughout the entire perimeter of the Gulf, but *C. parallelus* and *C. pectinatus* penetrate only to the north coast of Yucatán, northwestern Cuba, and southern Florida. *C. ensiferus* seems to be absent from Florida.

SHORE FISHES

There are certain species of coastal fishes which occur along the entire perimeter of the Gulf (except Cuba) but not in the West Indies proper. Some of these species are entirely confined to the Gulf, and others penetrate the Yucatán Channel and the Straits of Florida, extending along the mainland of Central America and the Atlantic coast of the United States, respectively. These species represent a small percentage of the total fish fauna of the Gulf and include tropical representatives as well as forms of northern origin. The well-known sheepshead (*Archosargus probatocephalus*), channel bass (*Sciaenops ocellatus*), and the common weakfish (*Cynoscion regalis*) among several others, are good examples illustrating this condition. These fishes are fairly common in the Gulf of Mexico including extreme south Florida, but they have never been reported from Cuba or any other of the West Indies. The ecological conditions prevailing in extreme south Florida are common to northwestern Cuba, and since many coastal species occur in both these areas, it is difficult to explain the absence of certain forms in Cuba. The species under discussion are not tropical, and it seems reasonable to assume that the Gulf Stream forms a temperature barrier preventing their dispersal into the West Indies. On the other hand, the Gulf Stream has been a very important temperature factor favoring the dispersal of most tropical West Indian fishes into the Gulf of Mexico, especially its southern portion. The percentage of species present in the Gulf of Mexico but absent in the West Indies is considerably higher than that of West Indian species absent in the Gulf.

As already pointed out, most of the shore fishes of the Gulf of Mexico also occur in the Caribbean Sea, and many of them are strictly stenobathic forms confined to shallow water and apparently unable to disperse across deep and wide water gaps. Despite this condition most of the species occur on both sides of the Yucatán Channel and the Straits of Florida. These deep and relatively wide water gaps would represent a bathic barrier to the adult fish but not to its pelagic or semipelagic larva as demonstrated for some of those species.

A third, very characteristic distributional pattern affecting several species is well illustrated by *Acipenser sturio* (common sturgeon) and *Dorosoma cepedianum* (gizzard shad). These species occur along the north and east shore of the Gulf of Mexico as far south as central Florida and reappear along the Atlantic coast of the United States, being absent around south Florida. This discontinuous distribution seems to be caused by the influence of the main branch of the Gulf Stream acting as a thermal barrier and preventing dispersal around the southern extremity of peninsular Florida. *Acipenser sturio* and *Dorosoma cepedianum* are temperate forms, and their presence on either side of peninsular Florida may be explained by the former continuity which existed between the Gulf of Mexico and the Atlantic Ocean across northern Florida during the interglacial periods of the Pleistocene. According to the paleogeographic evidence, this passage existed until relatively recent times.

Peninsular Florida and the main branch of the Gulf Stream may therefore be considered as land and thermal barriers, respectively, preventing at present the exchange of temperate fishes between the Atlantic Ocean and the Gulf of Mexico. The isolating effect of these barriers as a factor in speciation is well-illustrated by the shads, *Alosa sapidissima* and *A. alabamae*, of the Atlantic and Gulf coasts, respectively. These two very closely related, vicarious species seem to have evolved when the original ancestral population, continuous along the south coast of the United States, was split by the emergence of peninsular Florida. Neither *Alosa sapidissima* nor *A. alabamae* occur around south Florida. (See also Ginsburg, 1952, pp. 99–101.)

The paleogeographic evidence indicates that the Gulf of Mexico originated as a shallow basin and according to Schuchert (1935, p. 59):

"Previous to Middle Cretaceous time, it is believed, no such deep Gulf of Mexico as the present one was in existence, and the area now occupied by this suboceanic interior sea was a

gentle sag or flat platelike basin . . . With the Middle Cretaceous, the area commenced to subside . . . and this downward tendency persisted until the Gulf reached its present great depth and extent." [See also Lynch's article, pp. 67–86.]

It is therefore safe to assume that shallow-water or shore fishes were the first to become established in the Gulf of Mexico and that they constitute the oldest element of its ichthyological fauna.

As already indicated, the shore fish fauna of the Atlantic coast continued into the Gulf of Mexico before peninsular Florida was established as a barrier to many of the species during the Pleistocene. A connection with the Caribbean Sea through the Yucatán Channel was established during the Pliocene. It would seem, therefore, that the North Atlantic element became established in the Gulf before Caribbean fishes were able to disperse through the Yucatán Channel.

PELAGIC FISHES

As might be expected from the foregoing discussions, the pelagic fishes of the Gulf of Mexico are the same as those of the Caribbean Sea and adjacent parts of the Atlantic Ocean. They are mostly associated with the Gulf Stream, and the paleogeographic evidence would seem to indicate that their presence in the Gulf dates from relatively recent times.

DEEP-SEA FISHES

As already pointed out above, the Gulf of Mexico originated as a shallow basin. Bathic and other associated ecological conditions suitable to deep-sea fishes were not established until comparatively recent times. This would seem to indicate that the deep-sea fish fauna of the Gulf did not evolve in situ but was recently derived from the older, adjacent oceanic areas, such as the Caribbean Sea and the Atlantic Ocean. In fact, most of the deep-sea fishes of the Gulf of Mexico also occur in the Caribbean Sea and the Atlantic Ocean, and many of the species are cosmopolitan in distribution.

Owing to obvious collecting difficulties, deep-sea fish faunas are poorly known taxonomically as well as geographically, and further exploration may extend the range of a few species so far reported only from the Gulf of Mexico.

As already indicated in the introduction, the present depth of the Yucatán Channel and the Straits of Florida cannot be construed as barriers preventing the dispersal of deep-sea fishes to and from the Gulf.

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BIOLOGY OF THE COMMERCIAL FISHES OF THE GULF OF MEXICO

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The ecology of the fishes of the Gulf of Mexico differs in many respects from that of the Atlantic coast. The offshore waters of the Gulf (as indicated by current investigations by the Fish and Wildlife Service) are low in nutrients; the largest fish populations are thus found in the littoral zones where the nutrients necessary to grow the organisms forming the base of the food chain are washed from the land by rains and floods and carried in by rivers (Riley 1937).

At 1,200 fathoms the water masses in the Caribbean Sea are warmer and less dense than those outside the perimeter of the Caribbean. Those latter cold-water masses are derived from water that has sunk in high latitudes (Parr 1937, 1938). It therefore intermittently runs over the sills between the islands of the Antilles and flows down into the Caribbean and Cayman Basins. An intermediate water mass above 1,000 fathoms moves westward through the Caribbean between depths of 245 and 500 fathoms. This water, of Antarctic origin, is rich in nutrients. Between 100 and 250 fathoms the entering water is chiefly of South and North Atlantic central water origin.

There is little surface upwelling in the Caribbean, but on the Venezuelan coast the tilt of the water layers brings nutrient-rich waters up to the euphotic zone. The Gulf of Mexico derives its deep waters from water flowing from the Caribbean Sea over the sill in the Yucatán Channel which is not so deep as the main entrances to the Caribbean Sea. Proximity to this inflowing current may account for the productivity of the fisheries of the Campeche Banks.

Most of the new water entering the Gulf apparently flows out again through the Straits of Florida so that the main part of the Gulf is more or less of a cul-de-sac. This may influence the low nutrient content of the offshore waters of the Gulf.

As in most subtropical waters the high temperatures cause rapid growth. The same or related species in the Gulf tend to grow faster than on the northern Atlantic coast; they attain maturity at younger ages and are usually smaller in size. The life histories of many of the fishes of the Gulf are practically unknown. Some of those that occur both in the Gulf and along the Atlantic coast have been studied on the Atlantic coast, and presumably their life histories in Gulf waters are similar. Within the Gulf proper, mention should be made of the studies by Pearson, Gunter, and Gowanloch. However, the area is so vast, the species so numerous, and the conditions so diverse that the total knowledge is meager when compared to that of the Pacific or Atlantic coasts.

It is known that certain species can be caught in certain localities, but no detailed study is available on many of the most abundant species such as the menhaden, the anchovy, the Spanish mackerel, the groupers, and the snappers. Ginsburg (1930), in describing the biology of the common red snapper, *Lutianus aya*, says, "the red snapper is one of the important food fishes of this country. . . . Among the commercial food fish of the Gulf coast . . . the red snapper is second in point of quantity obtained, being exceeded only by the mullet . . . it is significant that practically nothing is known regarding the life history of the red snapper."

The relative abundance of the different species of fish is not accurately known, especially for those not landed by fishermen or only taken incidentally while in pursuit of other species. In estimating relative abundance, Gunter (1945a) uses the term "total species mass." He states that, "The estimates of relative species mass of the fishes given here are based on general impressions and observations, bolstered to some extent by data, and are admittedly more subjective than is desirable. It is quite certain, however, that irrespective of their rank in species mass, the species discussed are the most numerous fishes in Texas coastal waters." For the inshore fishes

of the northern and western Gulf, Gunter ranks the species as follows:

1. Anchovy, *Anchoa mitchilli diaphona.*
2. Mullet, *Mugil cephalus.*
   Menhaden, *Brevoortia* sp.
   Croaker, *Micropogon undulatus.*
3. Silverside, *Menidia beryllina peninsulae.*
   Sheepshead minnow, *Cyprinodon variegatus variegatus.*
4. Catfish, *Galeichthys felis.*
   Sandtrout, *Cynoscion arenarius.*
5. Red drum, *Sciaenops ocellata.*
   Speckled trout, *Cynoscion nebulosus.*
   Black drum, *Pogonias cromis.*

It will be noted that the species at the top of the list are preponderantly plankton feeders. They must form one of the chief layers in the food chain, linking the macroplankton to the predaceous fishes.

The food fishes in the Gulf I have grouped according to their habitat into at least five categories that seem to fit reasonably well with the known facts:

1. The bank fishes that are taken chiefly on the offshore banks. The best known is the red snapper, *Lutianus aya*, taken throughout the Gulf on numerous banks including the Campeche Bank.

2. Stenothermal species that are not found in abundance around the northern perimeter of the Gulf. This applies to many species in the Florida Keys such as the grunts (*Haemulon* spp.).

3. Inshore species whose abundance, because of their life history, is largely dependent on the ecological conditions in the inner bays and shallows. Examples are the red drum, *Sciaenops ocellata*, the croaker, *Micropogon undulatus*, and the mullet, *Mugil cephalus.*

4. Offshore species whose life histories make them more or less independent of the waters between the mainland and the barrier islands. These include the menhaden, *Brevoortia*, the pompano, *Trachinotus carolinus*, the butterfish, *Poronotus triacanthus*, and the Spanish mackerel, *Scomberomorus maculatus.*

5. Anadromous and estuarine species that either go into fresh water at certain times or live in fresh or brackish waters. Examples are the gizzard shad, *Dorosoma cepedianum*, the striped bass, *Roccus saxatilis*, the sea catfish, *Galeichthys elis*, and the snooks, (*Centropomus* spp.).

The offshore bank fishery has been described by Jarvis (1935). There are in reality two fisheries: one by small boats that fish along the shores of the Gulf, especially along the west coast of Florida and among the Florida Keys, the other by large vessels sailing from Pensacola and a few minor ports. These larger vessels also fish the shores of the Gulf out to the 100-fathom curve (but not close inshore). However, they take the bulk of their catch from the numerous offshore shoals lying north and west of Yucatán and known collectively as Campeche Bank.

In the waters fished by the offshore vessels (about 15 to 100 fathoms) the catch consists largely of groupers and snappers, the latter preferring the deeper water. Of the snappers the most abundant is the common red snapper, *Lutianus aya.* The silk or yellow-eye snapper, *Lutianus vivanus*, is caught in deeper water than the red snapper. The Caribbean red snapper, *Lutianus aya* (regarded by Ginsburg 1930, as a separate species), is fairly abundant on the eastern part of the Campeche Bank. The black-fin snapper, *Lutianus buccanella*, abundant in the Caribbean, is taken in small quantities from the deeper waters of Campeche Bank. The smaller vessels, when fishing in the shallower waters along the Florida coast and amongst the Florida Keys, take several other snappers, especially the gray or mangrove snapper, *Lutianus griseus*, the schoolmaster, *L. apodus*, the muttonfish, *L. analis*, the Lane snapper, *L. synagris*, and the yellowtail, *Ocyurus chrysurus.*

The offshore vessels also make large catches of groupers consisting principally of the red grouper, *Epinephelus morio.* Among the Florida Keys there are several groupers usually taken: the yellowfin grouper, *Mycteroperca venenosus*, the black grouper, *M. bonaci*, the gag, *M. microlepis*, the scamp, *M. falcata*, and the jewfish, *Promicrops itaiara.*

The fisheries in the vicinity of Key West are described by Schroeder (1924). The most striking feature is the large number of species taken among the Florida Keys and along the southern tip of Florida that are either absent or scarce in the northern Gulf.

The western and northern shores of the Gulf are fringed by narrow barrier islands and reefs that cut off long, shallow bays parallel to the

coast. Only a few narrow passes connect these inner bays with the open Gulf. Because of the low range of tide levels this results in weak circulation of water between the bays and the Gulf. As a result, these bays exhibit wide ranges in temperature and salinity. The rise in the rivers following the winter rains causes a great drop in salinity; many of the bays are almost fresh for periods of a few months. Many of them normally have a salinity around 15 to 20 parts per thousand contrasted with nearly 35 parts in open ocean water. During the winter a strong, cold, north wind occasionally drops the temperature very suddenly and many of the cold-sensitive fish are killed before they can reach deep water.

The importance of the passes connecting the bays to the open Gulf is shown by the life histories of many of the species. Thus, the redfish or red drum, *Sciaenops ocellata*, the croaker, *Micropogon undulatus*, the black drum, *Pogonias cromis*, the spot, *Leiostomus xanthurus*, and the striped mullet, *Mugil cephalus*, all important sport and commercial species, crowd through these narrow passes during the fall and early winter to reach the open Gulf. Here they spawn, chiefly in the vicinity of the passes. The post-larval and young of these species are later observed in vast schools entering the passes from which they spread throughout the shallow, inner bays. A few species, such as the spotted sea trout, speckled trout, or squeteague, *Cynoscion nebulosus*, spawn within the inner bays.

One of the most interesting areas biologically is the Laguna Madre, a narrow bay 115 miles long, paralleling the Texas coast. No rivers enter the Laguna, and its only present connection with the Gulf is through Corpus Christi Bay at the northern end. In depth it ranges from a few inches to 4 feet, with occasional deep holes. As a result of the shallow depths, the lack of permanent stream drainage, the high evaporation rate, and the poor connection with the Gulf, the monthly average salinity of the upper Laguna is above 50‰, and in some years salinities well over 100‰ are found.

Despite these conditions it produces a large quantity of fish. When the salinity rises above a critical point (about 72‰, Gunter 1945b) fish start dying by the thousands. This happens every few years. Because of the life histories of the species involved and the absolute necessity that the young find suitable conditions in the inside bays, perhaps the chief fishery problem of the region is the maintenance of proper conditions in these bays.

Because of the lack of any major streams the important feature in the Laguna Madre is the high salinity. The shallowness of the water makes it impossible to obtain any significant circulation through a narrow pass, no matter what its depth, so that the only major changes in salinity occur when there is a rise in the water level across the wide, northern entrance to Corpus Christi Bay. As the tide ranges are slight the extra high levels occasionally attained through the piling up of water by strong, inshore winds are of major importance to the circulation in the Laguna.

Excluding the Laguna Madre, most of the bays behind the barrier islands and reefs are entered by large rivers. The problem in these bays is, in part, similar to that of the Laguna. They differ, however, in that while high salinity is the problem in the Laguna, these other bays are troubled chiefly by low salinity. The difficulty has heightened with the passing years as soil erosion and sparse vegetative ground cover caused by overgrazing has intensified the magnitude of the floods. The problem in these other bays may be solved eventually through better agricultural practices and through flood control and power dams that will assure a steadier flow of fresh water. A certain amount of fresh water is needed to prevent conditions similar to those in the Laguna, but too much fresh water in a short period drops the salinity to almost zero. Because of the poor circulation these flood waters take many weeks to become mixed with water from the Gulf.

In addition to those species that depend on the ecological conditions in the inner bays, there are many species on the perimeter of the Gulf whose life histories, so far as known at present, render them more or less independent of conditions in the inner bays. These probably include the menhaden, *Brevoortia*, the pompano, *Trachinotus carolinus*, the butterfish, *Poronotus triacanthus*, and the Spanish mackerel, *Scomberomorus maculatus*. The actual degree to which any one species is dependent on the inside waters is at present largely a matter of speculation. The answer lies in continued research.

There are also many species of estuarine and anadromous fishes in the Gulf. Gunter (1945a)

TABLE 1.—*United States fish production in the Gulf of Mexico and eastern Florida in 1945*

[In thousands of pounds; based on Anderson and Power, 1950]

Species	Texas	Louisiana	Mississippi	Alabama	Florida	Total
Bank species (chiefly offshore):						
Red snappers, *Lutjanus* sp	288	26	12	1,361	3,092	4,779
Groupers	17	3	7	169	8,593	8,789
Bank and reef species (except offshore):						
Mangrove (gray) snapper, *Lutianus griseus*					214	214
Jewfish, *Promicrops itaiara*	12	2		3	423	440
Muttonfish, *Lutianus analis*					213	213
Yellowtail, *Ocyurus chrysurus*					330	330
Sea bass, *Centropristes* sp					101	101
Grunts, *Haemulon* sp					188	188
Pigfish, *Orthopristes chrysopterus*					157	157
Sharks	64	13			2,028	2,105
Inshore and pelagic species:						
Redfish, red drum, *Sciaenops ocellata*	1,297	596	66	260	2,053	4,272
Black drum, *Pogonias cromis*	1,213	301	19	141	986	2,660
Croaker, *Micropogon undulatus*	35	146	2	133	298	614
Spotted sea trout, *Cynoscion nebulosus*	1,680	639	102	370	4,376	7,167
White sea trout, *Cynoscion arenarius*	40	278	198	212	395	1,123
Spot, *Leiostomus xanthurus*		112	1		450	563
Sheepshead, *Archosorgus probatocephalus*	34	138		104	732	1,008
Pinfish, *Lagodon rhomboides*					157	157
Mullet, *Mugil* sp	95	76	156	3,356	34,528	38,211
King whiting, *Menticirrhus* sp	120	500	191	193	1,761	2,765
Spanish mackerel, *Scomberomorus maculatus*	14	2	7	70	10,638	10,731
Menhaden, *Brevoortia* sp			57,340		121,912	179,252
Oafftopsail, sea catfish, *Bagre marinus*	59	343		8	469	879
Snook, *Centropomus* spp	1				512	513
Tripletail, *Lobotes surinamensis*		2			63	65
Sawfish, *Pristis pectinatus*		15				15
Pompano, *Trachinotus carolinus*	4	1		4	766	775
King mackerel, *Scomberomorus* sp	22				3,897	3,919
Flounders	135	221	168	217	751	1,492
Amberjack, *Seriola* sp					376	376
Mojarra, *Gerridae*					183	183
Permit, *Trachinotus goodei*					1	1
Tenpounder, Bonefish, *Elops saurus*					613	613
Hogfish, *Lachnolaimus maximus*					15	15
Harvestfish, *Peprilus* sp					17	17
Dolphin, *Coryphaena hippurus*					83	83
Crevalle, Jack, *Caranx hippos*				62	536	598
Cigarfish, Scad, *Decopterus punctatus*					55	55
Butterfish, *Peronotus triacanthus*					27	27
Cabio, *Rachycentron canadus*				1	119	120
Blue runner, *Caranx* sp				2	1,982	1,984
Bluefish, *Pomatomus saltatrix*			1	31	1,831	1,863
Barracuda, *Sphyraena* sp					46	46
Tarpon, *Torpon atlanticus*						
Anadromous species:						
Alewives, *Pomolobus* sp					428	428
Gizzard shad, *Dorosoma cepedianum*					550	550
Hickory shad, *Pomolobus mediocris*					86	86
Shad, *Alosa sapidissima*					842	842
Striped bass, *Roccus saxatilis*						
Brackish and fresh-water species:						
Garfish, *Lepisosteus* sp		22				22
Catadromous species:						
Eels, common, *Anguilla bostoniensis*					60	60
Grand totals	5,130	3,436	58,270	6,697	207,393	281,466
Recapitulation:						
Bank species (chiefly offshore)	305	29	19	1,530	11,685	13,568
Bank and reef species (except offshore):						
Sharks	64	13			2,028	2,105
Others	12	2		3	1,626	1,643
Total	76	15		3	3,654	3,748
Inshore and pelagic species:						
Menhaden			57,340		121,912	179,252
Mullet	95	76	156	3,356	34,528	38,211
Sciaenids (drums, croakers, spot)	2,665	1,655	279	727	5,548	10,874
Spanish mackerel	14	2	7	70	10,638	10,731
Weakfishes	1,720	917	300	582	4,771	8,290
Carangids (jacks and pompanos)	4	1		68	3,340	3,413
Porgies (sheepshead and pinfish)	34	138		104	889	1,165
King mackerel	22				3,897	3,919
Bluefish			1	31	1,831	1,863
All others	195	581	168	226	3,274	4,444
Total	4,749	3,370	58,251	5,164	190,628	262,162
All other categories		22			1,966	1,988

shows that several species are taken only at very low salinities, while many species are taken both at low and at high salinities. Information is lacking as to whether the abundance of the latter group is dependent on low salinities. It may be that the nutrients carried by the rivers are of much greater importance than the salinities in determining both distribution and abundance.

The statistics on the catch are contained in the following table. Unfortunately, the Atlantic and Gulf coasts of Florida are not separable. Most of the Florida catch is from the Gulf coast and the Florida Keys. Out of a total catch of 281 million pounds, 179 million were menhaden, leaving only 102 million pounds of food fish for the five States.

Of the food fishes Florida produced 86 million pounds against only 16 million for the other four States. Considering the long coast line involved, this is a very small fishery.

Probably the chief problem now confronting fishery biologists in the Gulf is to ascertain the cause of the low productivity of the fin-fish fisheries. It may be more than mere chance that the greatest producing areas are where the two prongs of the land, the Florida and Yucatán Peninsulas, project close to the currents that flow from the Caribbean Sea into the Gulf and then turn eastward to flow out of the Straits of Florida.

The important shrimp fisheries appear to depend on nutrients from the land. The young shrimp are reared in the shallow marshes, and the older shrimp live on the mud bottoms, especially on both sides of the present Mississippi Delta and on bottom that was part of former deltas.

From the accounts of the fishery explorations and of the red snapper fisheries one gains the impression that the bottom fisheries of the Gulf are incapable of any large expansion. There remain then, unless further research proves otherwise, two sources of possible expansion. One is the tremendous potential productivity of the inner bays if the problems of fluctuating salinities can be solved. The other lies in the expanded exploitation of the pelagic fishes, especially those subsisting on the plankton, such as the menhaden, the anchovies, and other clupeids. Only exploitation will tell us whether these fishes can support a large catch.

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TAXONOMY AND DISTRIBUTION OF SEA TURTLES[1]

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Out of the total of nine species of living turtles found throughout the world, five occur in the Gulf area. Only three of these are normally found in the Gulf of Mexico in sufficient quantity to be of any commercial value. These are the green turtle, *Chelonia mydas* (Linné), the loggerhead turtle, *Caretta caretta* (Linné), and the hawksbill turtle, *Eretmochelys imbricata* (Linné). The bastard turtle or Kemp's turtle, *Lepidochelys kempii* (Garman) and the leatherback or trunk turtle, *Dermochelys coriacea* (Linné) are comparatively few so that they have at no time been of economic importance.

Considerable confusion existed at one time regarding the nomenclature. This arose from the wide distribution of some of the species and the comparative isolation of workers in various parts of the world. The work of Stejneger and Barbour (1943–44) based upon a number of collections is used here as a basis for the systematic arrangement. A more comprehensive list of synonyms and authors is given in the earlier work of Garman (1884).

Family CHELONIIDAE

***Chelonia* Latreille**, Hist. Nat. Rept., vol. 1, 1801, p. 22.
(Type: *mydas*)

***Chelonia mydas* (Linné).** Green turtle

***Testudo mydas* Linné**
Syst. Nat., Ed. 10, vol. 1, 1758, p. 197.

***Chelonia mydas* Schweigger**
Königsberg. Arch. Natur. Math., vol. 1, 1812, Pt. 3, p. 412.

Type locality: Ascension Island.

Range: Atlantic Ocean; Gulf of Mexico; occasionally as far north as Massachusetts.

***Eretmochelys* Fitzinger**, Syst. Rept., 1843, p. 30.
(Type: *imbricata*)

***Eretmochelys imbricata* (Linné).** Hawksbill turtle

***Testudo imbricata* Linné**
Syst. Nat., Ed. 12, vol. 1, 1766, p. 350.

***Eretmochelys imbricata* Agassiz**
Contr. Nat. Hist. U. S., vol. 1, 1857, p. 381.

Type locality: American seas.

Range: Florida and Gulf coasts; occasionally as far north as Massachusetts.

***Caretta* Rafinesque**, Specchio Sci., Palmero Vol. 2 No. 9, Sett. 1, 1814, p. 66.
(Type: *carctta*)

***Caretta caretta* (Linné). Atlantic loggerhead turtle**

***Testudo caretta* Linné**
Syst. Nat., Ed. 10, vol. 1, 1758, p. 197.

***Caretta caretta* Stejneger**
Ann. Rep. U. S. Nat. Mus., 1902 (1904), p. 715.

Type locality: "About the American Islands."

Range: Atlantic Ocean, breeding as far north as Beaufort, North Carolina; north occasionally to coast of Massachusetts.

***Lepidochelys* Fitzinger**, Syst. Rept., 1843, p. 30.
(Type: *olivacea*)

***Lepidochelys kempii* (Garman). Kemp's, Mexican or loggerhead**

***Thalassochelys* (*Colpochelys*) *kempii* Garman**
Bull. Mus. Comp. Zool., vol. 6, 1880, p. 123.

***Lepidochelys kempii* Baur**
Am. Naturalist, vol. 24, 1890, p. 487.

***Caretta kempii* Stejneger and Barbour**
Check List N. Am. Amph. Rept., Ed. 4, 1939, p. 170.

Type locality: Gulf of Mexico.

Range: Northern part of Gulf of Mexico north to Cape Hatteras, and occasionally, to the coast of Massachusetts, the Azores, and the coast of Ireland.

Family DERMOCHELIDAE

***Dermochelys* Blainville**, Bull. Soc. Philom. Paris, 1816, pp. 111–119.
(Type: *coriacea*)

***Dermochelys coriacea* (Linné). Leatherback or trunk turtle**

***Testudo coriacea* Linné**
Syst. Nat., Ed. 12, vol. 1, 1766, p. 350.

***Dermochelys coriacea* Boulenger**
Cat. Chel. Brit. Mus., 1889, p. 10.

Type locality: Mediterranean Sea.

Range: Atlantic Ocean, occasionally on entire coast as far north as Nova Scotia.

Turtles usually possess bony plates covering the outer surface of the body. The plates are fused so as to form a rigid shell which may or may not be covered with horny shields. The dorsal portion is referred to as the carapace and the ventral as the plastron.

Dorsally along the median line there is a row of plates, known as the neurals, which are fused

[1] Contribution No. 108 from the Marine Laboratory, University of Miami.

with the vertebrae. The anteriormost of this is the nuchal. Lateral to the neurals are a paired series of plates which fuse with the ribs. These are the costals. The outermost edge of the carapace, enclosing the costals, consists of a series of plates called the marginals.

Green turtles.—These are characterized by a single pair of large shields, the prefrontals, on top of the head and between the eyes. Four costal only are present on each side. The shields of the carapace do not overlap as they do in the hawksbill except slightly when very young, and the margin of the carapace is smooth. The limbs are paddle-shaped and possess only one claw except in occasional aberrant individuals which have two.

The tail of the female barely reaches beyond the margin of the carapace. The tail of the male reaches some distance beyond. The eggs are soft-shelled and white in color and not quite spherical, between 40 and 46 mm. in diameter.

The size does not usually exceed a carapace length of 36 inches and a weight of 200 pounds, although 850 pounds has been recorded.

The green turtle is valued principally for use as food.

Hawksbill turtles.—Like the green turtles, these have only four pairs of costal shields. They differ in that they overlap, and the overlapping edges are rough and serrated. The margins of the carapace are markedly serrate, each marginal shield projecting from the posterior end as a pointed extremity. The marginal serration is less noticeable on the anterior end of the animal. Two pairs of large shields, the prefrontals, are located between the eyes on top of the head. The paddle-shaped limbs are each equipped with two claws, rarely one. The jaws form a hooked beak from whence the name "hawksbill" is derived.

Sexual dimorphism of the tail is the same as in the green turtle. In males the two shields in the center of the top of the head, the frontal and frontoparietal, are separate. In the female they are fused. Eggs are 38 to 41 mm. in diameter, white, with a mucilaginous coating.

Loggerhead turtles.—The distinguishing feature in these turtles is the presence of five or more pairs of costal shields instead of the four pairs in the hawksbill and green turtles. Two pairs of large shields, the prefrontals, are found on the top of the head between the eyes. Five or more costal shields are present on each side, the first one of each row making contact with the nuchal. Limbs are paddle-shaped, each with two claws. Sexual dimorphism of the tail is a feature of this species, similar to the leatherback. Eggs are approximately 42 mm. in diameter and are white and soft. Deraniyagala (1943, 1945) has good evidence that the loggerhead has broken up into several subspecies or races.

Kemp's loggerhead is distinguished by being olive green in color dorsally, whereas the Atlantic loggerhead is brown or red. The former possesses four enlarged inframarginal shields along the outer edge of the marginals. Each of these has a pore. The neurals are equilateral in a continuous series. The Atlantic loggerhead, on the other hand, has only three enlarged inframarginals which do not possess pores. The neurals in this species have elongated posterolateral sides and are sometimes interrupted by costae. The Atlantic loggerhead has two-clawed limbs. Those of Kemp's turtle are three-clawed. Three and a half feet is a good length for the carapace of the loggerhead. The weight rarely exceeds 350 pounds. Kemp's loggerhead rarely exceeds 2 feet in length. It is not of commercial importance. It is nevertheless edible although inferior to the green turtle.

Leatherback turtles.—The carapace of this species is soft and free from the vertebrae and ribs. It is covered with smooth skin instead of horny shields. Seven prominent ridges extend down the back. In the male the tail extends beyond the hind limbs when extended. The eggs are soft and white and from 50 to 56 mm. in diameter.

KEY TO THE GULF OF MEXICO SEA TURTLES

1. Back is covered with leathery skin. — Leatherback, Luth, or Trunk Turtle *Dermochelys coriacea*
   Back covered with shields or plates 2
2. Five pairs of shields or plates along the back. Color uniformly brown, black, or olive green 3
   Four pairs of shields or plates along the back. Color brown or black mottled with yellow 4

3. Inframarginals three, without pores, two-clawed, brownish.	Atlantic Loggerhead Turtle *Caretta caretta*
Inframarginals four, with pores, three-clawed, olive green.	Kemp's Loggerhead Turtle *Lepidochelys kempii*
4. Shields do not overlap. Usually only one claw on front flipper. Jaw not beak-like.	Green Turtle *Chelonia mydas*
Shields do overlap. Two claws on front flippers. Upper jaw forms overhanging beak.	Hawksbill Turtle *Eretmochelys imbricata*

DISTRIBUTION IN THE GULF OF MEXICO

The building of harbor works, the increasing human populations in the immediate proximity of the sandy beaches used for turtle nesting, and heavy fishing in the past have all contributed to the decline in numbers of all species of marine turtles in the Gulf of Mexico. The populations have now been reduced to the point where the commercial utilization of the more common green turtle is purely local in extent and limited principally to the Florida Keys. Most of the turtles landed in Florida today are shipped from Nicaragua or from the Cayman Islands.

The green turtle is still seen frequently in the Florida Keys, but is no longer common in the western or northern part of the Gulf of Mexico although seen occasionally. This marks a definite decline in numbers, since 3,500 pounds of green turtle were landed in Louisiana in 1936. Since then the catch has declined and is no longer reported. In Texas the most recently reported catch is for 1925 when 2,550 pounds were landed. This may be contrasted with landings of 90,793 pounds in Louisiana and 83,000 pounds in Texas during 1890. In the same year 468,256 pounds were landed in Florida. This is now reduced to less than 50,000 pounds, a large proportion of which is imported.

The hawksbill turtle has similarly declined. These are present throughout the Caribbean and are still to be seen frequently in the Florida Keys. They are not common anywhere else in the Gulf of Mexico.

The Atlantic loggerhead turtle is most often found, although not abundantly, in the Gulf of Mexico, more so off the eastern shores and the Florida Keys. Kemp's loggerhead is rarely recorded, possibly because it may be confused with the Atlantic loggerhead. It is found occasionally on most parts of the Gulf coast and rarely on the Atlantic coast.

The leatherback turtle is widely distributed throughout the tropical and subtropical seas. It is nowhere common, however, and is rarely seen today in the Gulf of Mexico. Since it prefers deep water to the shallow bays and lagoons, there is less opportunity for observing it, and this may partially account for its apparent rarity.

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CHAPTER XVIII
THE BIRDS OF THE GULF OF MEXICO

THE BIRDS OF THE GULF OF MEXICO[1]

By GEORGE H. LOWERY, JR., and ROBERT J. NEWMAN, *Museum of Zoology, Louisiana State University*

Birds are unlike any other class of animals in their relationship to water as an environment. Although some of them are absolutely dependent upon the sea for their existence, none of them is a creature of that medium in the same sense that a marine invertebrate is, or even a marine mammal such as a whale. All sea birds come to land to nest; and, in North America, all of them spend a part of their lives in the air. The birds of the Gulf of Mexico are thus, without exception, adapted to at least two media and endowed with a mobility that frequently makes their spacial and ecological classification difficult. None of them is wholly "pelagic" in the narrowest sense, and none of them wholly "littoral."

To make matters more difficult, the area delimited by the salt water of the Gulf of Mexico as it twice daily moves landward over the shores of the North American continent and up the tidal estuaries is a somewhat vague one. Its ill-defined boundaries have been crossed, and are daily being crossed, by hundreds of different kinds of birds. The overwhelming majority of these birds are really birds of the mainland, whose occurrence on the Gulf is wholly marginal. As a result, the Gulf and its tidal reaches present a vast interior surface, with a very limited avifauna, contained within a narrow rim around which birds occur in profusion.

This distributional pattern introduces serious problems when one attempts to summarize the bird life of the Gulf of Mexico, problems that are not encountered in the same degree in the case of more sedentary groups of animals, or even in the case of the avifauna of terrestrial regions. The conventional summary of the bird life of a land area seeks to review all the species that have been known to occur there, to provide the visitor to that area with a reference to the status of every bird that he is likely to observe. As long as we are dealing with the waters of the open Gulf, we can employ much the same approach, mentioning all the species that have been found offshore. But the moment we turn to the intertidal zone, such a treatment becomes impossible. Too many of the records on which our judgments must be based do not include information on the proximity of the bird to tidewater. And, even if such information were available, the comprehensive approach would scarcely be desirable, for it would lead to a survey in which only a minor part of the species considered would be birds that are regularly and intimately associated with the Gulf itself.

Since birds differ so tremendously in their relationships with water and since their relevance to a discussion of the Gulf avifauna is so variable in degree, we have divided the species that we shall consider into three groups, each of which will be accorded a different type of treatment. These groups are: I. Offshore Birds; II. Birds of the Coast; III. Land Birds Over the Open Gulf.

Groups I and III, it will be noted, both chiefly represent the main expanse of the Gulf of Mexico, a portion of the earth's surface whose bird life has never been comprehensively reviewed. We have tried to mention every species in these groups in order to make the corresponding sections of the chapter a fairly complete reference source for bird students traveling on the open Gulf. The available data concerning land birds offshore can conveniently be compressed into tabular form, and this has been done. The status of the so-called pelagic species, on the other hand, being more complex, requires fuller discussion.

The birds of the littoral present a fundamentally different situation, since they cannot be defined in concrete spacial terms. Completeness becomes a less important concern in this group for reasons later to be emphasized. Consequently we have not hesitated to omit some species that have actually come in contact on occasion with the water of the Gulf itself. Even so, our list of coastal species is so long that, in order to adapt the ac-

[1] Manuscript submitted for publication March 1952.

count to the available space, it has been necessary to use a summary written in telegraphic style.

There is a fourth group of birds whose distribution is affected by the Gulf of Mexico. These are the land birds of the Gulf islands. This group, however, is so large and so varied that it must be considered beyond the scope of this chapter.

Illustrations and condensed field marks for all of the birds included in these categories, except a few species occurring in western Cuba and on the coast of Mexico, are to be found in Peterson (1947). The Cuban species are concisely described in Bond (1936, 1947), and the Mexican species are among the birds briefly discussed by Sutton (1951). The several volumes of The Birds of North and Middle America (Ridgway 1901–19; Ridgway and Friedmann 1941, 1946; Friedmann 1950) offer the best technical keys and technical descriptions available for identifying a specimen in the hand. When completed, this work will include all of the birds of the Gulf of Mexico. Unfortunately several important orders, including such birds as the ducks, herons, ibises, pelicans, boobies, shearwaters, and petrels remain to be treated. Meanwhile, most of the gaps may be filled by recourse to the older keys in Ridgway (1900). The revision of Pratt's Manual of the Vertebrates, now in course of preparation, will also provide keys to all the birds of the Gulf that occur in the United States.

In preparing the distributional summaries contained in this paper, we have drawn freely on the published and unpublished work of many ornithologists. To include references for every quoted item would not only seriously lengthen the text but would interfere with its continuity. Many recent data relating to the birds of the Gulf have been taken from the appropriate sections of Bird-Lore's The Season, and its successor Audubon Field Notes (Weston 1924–48; Davis 1936–40; Williams 1941–51; Brookfield 1949–51; Lowery and Newman 1949–51). Most of the remaining published data included here, unless otherwise accredited, are to be found in the following works: Cuban records in Barbour (1943) and Bond (1936, 1950); Florida records in Howell (1932); Alabama records in Howell (1924); Mississippi records in Burleigh (1944); Louisiana records in Oberholser (1938); Texas records in Griscom and Crosby (1925–26); Mexican records in Friedmann et al. (1950), and Sutton (1951).

We wish to express particular thanks to Fred M. Packard and Mrs. Conger Hagar and to Dr. Frederick W. Loetscher, Jr., for permission to consult their splendid manuscripts dealing respectively with the birds of the central Texas coast and with the ornithology of Veracruz. The first draft of the present paper was mimeographed, and copies were sent to more than 30 zoologists, each of whom is intimately acquainted with the bird life or the marine ecology of one or more sections of the Gulf's periphery. In response, a wealth of critical suggestions and of useful data drawn from unpublished notes was received from the following: Ellinor H. Behre, H. J. Bennett, James Bond, Charles M. Brookfield, Jas. Hy. Bruns, Harvey R. Bullis, Thomas D. Burleigh, L. Irby Davis, Herbert Friedmann, Gordon Gunter, R. C. Hallman, Joseph M. Heiser, Julian A. Howard, Frederick C. Lincoln, John Lynch, Merriam L. Miles, Robert C. Murphy, Harry C. Oberholser, Raymond A. Paynter, Jr., J. H. Roberts, Chandler Robbins, Alexander Sprunt, George M. Sutton, Henry M. Stevenson, Herbert Stoddard, Robert W. Storer, J. Van Tyne, Francis M. Weston, A. Wetmore, and George G. Williams. Without the information obtained from these sources, a much less balanced picture of the bird life of the Gulf coast would have resulted.

I. OFFSHORE BIRDS

The birds of any ocean that seem most truly its own are those so perfectly adjusted to a life on the open sea that they cannot long survive away from it. Although they usually live on or over the water, rather than in it, such birds form a direct adjunct to the pelagial community. They variously derive their sustenance from food chains that begin with the diatoms and brown algae of the lighted upper stratum of the sea, and, when they die, their bodies return to the water to aid in maintaining its fertility. In some ecologic classifications of sea birds, a distinction is made between species that chiefly inhabit the surface of the Neritic Province, above the continental shelf, and those commonly found out over the deeper water of the true Oceanic Province. In the present state of our knowledge of Gulf ornithology, such a distinction is scarcely profitable or practicable. For the purposes of this summary, the primary group of sea birds will be called

simply "offshore birds" and defined as those species that only rarely come close enough inshore for an observer on the mainland to see them.

So varied are the relationships of birds with their environment that even this simple definition is not without difficulties in practice. To begin with, it sets up a criterion that is fundamentally distributional rather than ecologic. The brown pelican, for example, often flies out to fish the same waters as the gannet. It spends a great deal of its time, however, resting along the beaches or in the quiet water of the bays. And so we have placed it with the coastal birds. The gannet, on the other hand, while it is linked to much the same food chain as the pelican, almost never comes in to the land or to the harbors. And so we have considered it an offshore bird. Moreover, so little is known about the real distribution of sea birds over the Gulf that in many cases their very presence is merely inferred from their occurrence in coastal situations after storms. In instances of this sort, the species can be recognized as pelagic only by reference to its habits in other oceans. On this basis, the scoters do not, perhaps, strictly fit the definition of an offshore bird, since farther north on the Atlantic seaboard, they are regularly observed from land. But in the Gulf, where there are long shallows, we are inclined to regard the occasional appearance of a few birds inshore as a probable indication of their much commoner occurrence on the deeper water out beyond the range of vision. The old-squaw, as another example, is usually thought of as a sea duck in the same sense that the scoters are; yet in the southern States there have been more records of the species inland than on the Gulf. Consequently, we have felt that the old-squaw does not qualify as an offshore Gulf bird. As these illustrations serve to show, some of the groupings of birds that follow are based on an interpretation of meager facts, are necessarily somewhat arbitrary, and are to be considered merely provisional.

Even when one employs this rather liberal interpretation of the term offshore, the list of Gulf birds that can be included in that category is a modest one. It amounts to but 24 species, and on the basis of current evidence, only about one-half of them can safely be presumed to occur regularly every year. Not a single one of these species has yet been formally recorded on the Gulf in every month of the year, although reports of the white-bellied booby are lacking only in November. Of the other 11 kinds of birds that probably can be found there annually, 7 appear on the face of the record to be winter visitants and 4 to be summer visitants. The seasons of the summer and winter birds overlap in both spring and fall, and it is during these periods, when the domain of the sea birds is invaded by migrant birds of the land and the littoral, that the true pelagic avifauna reaches its own peak of variety and abundance. Only three pelagic species, the blue-faced booby and the sooty and noddy terns, are known to nest at present within the confines of the Gulf.

Ornithologically, as well as by other standards, the Gulf of Mexico is a tropical sea. Its breeding pelagic avifauna consists entirely of species that reach the northern limits of their normal range over its waters, and its scattered offshore islands [1] all lie in or near what has been termed the Lower Arid Tropical Life-zone. Thus the Gulf may be expected to share a characteristic feature of warm oceans by presenting vast expanses of surface that are virtually without birds. This condition results in part from a well-known principle. The higher the temperature of the water, the lower is its capacity, per given volume, to hold gases and the lower, therefore, its capacity to support the plankton upon which the food potentialities of the sea ultimately depend. As a result of these and other factors, the plant and animal life of the tropical oceans tends to be distributed in depth instead of concentrated in the upper stratum, and it is only where conditions cause a constant upwelling of water from the lower levels bringing up nutrient salts that surface feeders such as birds find an adequate food supply. Such a vertical mixing of strata is likely to occur where two currents come in contact or in the vicinity of islands.

While the breeding birds of the Gulf are all tropical, its pelagic avifauna as a whole is derived in about equal proportions from the north and the south. Many sea birds, however, that occur commonly in the upper latitudes of the North Atlantic, such as the fulmar, skua, and most of the Alcidae, seem to reach the southern limit of their ranges off New England or New Jersey,

[1] The term "offshore," as applied to islands in this paper, is used to designate those islands separated in all directions from the mainland by 25 miles or more of open sea.

where the cool Labrador current is met by a barrier of warm water. Even some northern species that penetrate this barrier and other species that wander up into the North Atlantic from below the equator never seem to get into the Gulf. Indeed, the whole offshore bird list of the Gulf, including accidentals, is only about one-half that of the North Atlantic from which it is drawn. The fact that the Gulf of Mexico is almost a closed sea is perhaps a factor in this result. In order to reach its waters, those sea birds that are reluctant to fly overland must thread their way through the maze of the Antilles and pass through the comparatively narrow portals of the Florida Straits or the Yucatán Channel. An interesting contrast, bearing on this point, is provided by the bird life of the Pacific Ocean within the same latitudinal limits, off the west coast of Mexico. Here, where there are different patterns of currents, a greater proximity to cool water, and no land barriers, 42 species of pelagic birds have been recorded, at least 22 of them as breeders.

The fact that the greatest superiority of the waters off western Mexico is in breeding birds, suggests that the nature of the associated offshore islands plays an important part in limiting the Gulf avifauna. With the exception of Cuba, most of which is extralimital to this summary, all of the islands of the Gulf lie within the limits of the continental shelf, and therefore outside the Oceanic Province which is often considered the real habitat of pelagic birds. The most remote of them are small coral formation situated below latitude 25°. On the Campeche Bank there are seven islets or atolls of this sort scattered at varying distances of 70 miles or more from the mainland. Among these is Cayo Nuevo, which, lying 125 miles in a northwesterly direction from Yucatán, has the distinction of being the farthest offshore of all the Gulf islands. Alacran Reef, however, although it is only about 80 miles north of the Yucatán Peninsula, is the most distant from all other land, including other islands. The only other really offshore islets are the Dry Tortugas, 110 miles off the coast of peninsular Florida but only 68 miles from the termination of the main arc of the Florida Keys at Key West.

Whether or not all eight of these offshore island groups offer suitable nesting sites is not known. The Tortugas, the Alacran Reef, and the Arcas and Triangle Keys are the only groups that have been reported on by ornithologists. The first three are definitely known to support sea bird colonies. The Triangle Keys are inhabited by a rare tropical seal (*Monachus tropicalis*), but whether it interferes with the colonization by birds is open to serious question. None of these islands is more than half a mile long or a few hundred yards wide, and, in view of their small numbers, the total area of dry land in the open Gulf must be so limited that it imposes serious restrictions on the breeding population of offshore birds. The sooty tern, it is true, is alleged to have once been established on Mujeres Island and the noddy tern on both Mujeres and Contoy Islands; but, although these islands are close inshore, they happen to be situated very close to the edge of the continental shelf.

Few aspects of field ornithology afford such opportunities to the general observer as the distribution of pelagic birds over the Gulf. Our present meager knowledge of this group of birds is reflected in the extremely imperfect summaries that follow.

Sooty Shearwater *Puffinus griseus.*

An occasional visitant to the Gulf, reported seven times from Florida (Pensacola; Pavilion Key; Florida Keys and adjacent waters), once from Texas (Aransas Bay, June 16–19, 1937), and from adjacent Cuban waters (Matanzas). Curiously enough, three of these occurrences were in winter, when the species is engaged in its breeding activities thousands of miles away in the Southern Hemisphere. The dates of occurrence in the Gulf proper range from December 29 to July 18 and involve every intervening month except February. The Texas record is substantiated by a photograph, and one of the Pensacola records (that of January 3, 1935) by a bird found dead on the beach; the other reports are based upon sight identifications, not all of which were positively assigned to this species by the observer. Apparrently, there is no Gulf specimen extant.

Audubon Shearwater *Puffinus lherminieri.*

A breeding bird of the West Indies, said to occur more or less regularly in the Gulf, but apparently not observed there alive since the time of Audubon, who claims to have seen it in numbers in June off the western shores of Florida.

The only modern record in the Gulf seems to be that of a dead bird picked up on Brazos Island, Texas, on January 28, 1947 (Davis 1951, p. 333).

Greater Shearwater *Puffinus gravis.*

One record for the Gulf proper: a specimen found on Dog Island, near St. Marks, Florida, January 29, 1950, and preserved in the Florida State Museum (Stevenson, 1950b, p. 71). This shearwater has also once been noted in the Straits of Florida between Key West and Havana (Bond 1950, p. 2).

Leach Petrel *Oceanodroma leucorhoa.*

Rarely identified in the Gulf. The only records are those of Danforth (1935, p. 74), on a voyage from Puerto Rico to Galveston, Texas, in 1932. He identified a petrel of this species in Cuban waters south of the Dry Tortugas on June 1 and saw several others in the Gulf on the following 2 days. At a point 200 miles from Galveston, observations of the Leach petrel abruptly ceased and gave way to those of the Wilson petrel. No specimens were secured, but 2 years later, also in June, Danforth shot a Leach petrel half a mile off Cayo Francés, Cuba, the nearest point to the Gulf where the species has been taken.

Wilson Petrel *Oceanites oceanicus.*

The commonest of the Procellariformes in the Gulf, where it appears widely during its nonbreeding season (records between Key West and Havana, off Dry Tortugas, off Pensacola, off Alabama, off southeastern Louisiana, off Texas, and off the coast of Veracruz). The known seasonal limits are April to the first week of September.

Black-bellied Storm Petrel *Fregetta tropica.*

An accidental straggler from the South Atlantic and Indian Oceans, only once recorded in North America, in 1851, when seven specimens were captured with a hook and line from a vessel at anchor in the harbor at St. Marks, Florida. The whereabouts of these specimens is not known.

Yellow-billed Tropic Bird *Phaëthon lepturus.*

A casual visitant from the Antilles, where it breeds. The seven definite reports in the last 130 years are scattered around the Gulf: three records in the Dry Tortugas (including Mason and Longstreet, 1936, pp. 19, 42); one at St. Marks, Florida; two at Rockport, Texas, and vicinity; and one on the open sea, 109 miles north of Progreso, Yucatán (Bullis, in litt.). Dates include January, May, June, and August. The alleged "almost common" occurrence of this species in Louisiana in midsummer has not been supported by further evidence. There are no Gulf specimens extant.

Blue-faced Booby *Sula dactylatra.*

Breeds 60 miles north of Yucatán, on Pajaros and Chica Islands in the Alacran Reef, where some 50 pairs had eggs and downy young on May 20, 1912 (Kennedy 1917, pp. 42–43). The species occurs regularly, but in sparing numbers (maximum number seen in recent years, nine), on the Dry Tortugas, and has been recorded also from the coasts of northwest Florida, Louisiana, Texas, and Tamaulipas. The dates range from March 22 to September 9.

White-bellied Booby *Sula leucogaster.*

Formerly bred abundantly on the Dry Tortugas, where eggs and young were observed by Audubon on May 14, 1832; not now known to breed closer to the Gulf than Piedras Island on the Caribbean side of Cuba, but still a regular visitor to the Tortugas in somewhat larger numbers than the blue-faced booby. The numerous Gulf records, which also include observations or specimens from the Florida Peninsula, the northern Gulf coast, the central Texas coast, northeastern Tamaulipas, the Bay of Campeche, and the waters off northern Yucatán, involve every month in the year except November.

Red-footed Booby *Sula sula.*

Found breeding extensively in the Caribbean area, but only twice definitely recorded from the Gulf or its immediate environs. A specimen was taken near Rockport, Texas, sometime prior to 1910, and another was secured near the mouth of the Mississippi River, 7 miles below Buras, Louisiana, on November 1, 1940 (Lowery, 1947, p. 180).

Gannet *Morus bassanus*

Seemingly a rather common winter visitant to the Gulf; extreme dates November 22 (Pensacola) to July 27 (12 miles northwest of Key West). At Pensacola, where the species can frequently be observed from the beach, F. M. Weston has noted

an increase in numbers over the past 20 years. His counts have run as high as 51 for a 45-minute period, and he has noted that the typical ratio is about 12 of the brown immatures to every black and white adult. There is only one definite record each for the coastal waters of Mississippi, Louisiana, and Veracruz; three for Alabama and Texas; and four for the Dry Tortugas or the adjacent waters. Gannets have also been seen at various points on a direct line between the mouth of the Mississippi Delta and Yucatán, in April and May.

White-winged Scoter *Melanitta deglandi.*

A winter visitant (October 20 to April 17), once recorded in August (Rockport, Texas). The 22 records from the Gulf area—6 from Florida, 1 from Alabama, 9 from Louisiana, 6 from Texas—involve a total of 31 birds. The most recent dates are November 12, 1950, at Pensacola, Florida; December 23, 1950, at Cameron, Louisiana; November 3, 1951, in St. Bernard Parish, Louisiana; and December 9, 1951, at Cove, Texas. All of the birds have been observed from the shore, or a few miles inland, and, since elsewhere scoters occur most abundantly at sea beyond the range of vision of mainland observers, these records may be indicative of much commoner occurrence offshore.

Surf Scoter *Melanitta perspicillata.*

Winter visitant, recorded from September 10 to March 12. There are 11 definite records—3 from Florida, 3 from Alabama, 3 from Louisiana, and 2 from Texas. The most recent observations are November 11, 1950, at Cove, Texas, and December 26, 1950, at Grand Isle, Louisiana. All of these observations are from close inshore, but general statements quoted by Howell (1924, p. 65) indicate that the surf scoter has occurred in flocks of 50 to 75 in the sound near Coffee Island, Alabama.

American Scoter *Oidemia nigra.*

Less frequently reported than the other scoters, but seen in greater numbers. Prior to 1948, there was but a single observation on the Gulf, that of a flock of 75 on April 15, 1938, 75 yards off the shore at Holly Beach, Cameron Parish, Louisiana (Lowery, unpublished notes). More recently there have been reports from three additional localities: Alligator Point, Florida, (5 birds on June 26, 1948; 70 on March 18, 1949; 48 on March 19, 1949); Cove, Texas (single birds killed on November 11, 1950, and November 9, 1951); and Rockport, Texas (4 on January 13, 1950, and 1 on January 28, 1950).

Red Phalarope *Phalaropus fulicarius.*

A winter visitant, noted from October 13 to March 17, in the northeast sector of the Gulf. Although the species has only twice been observed on the beach, it is of fairly abundant annual occurrence 5 to 40 miles offshore from Pensacola. On January 15, 1950, for example, flocks numbering up to 25 were encountered there throughout the day. The largest flock noted was a close aggregation of about 300 on February 29, 1948. There are no records elsewhere in the Gulf.

Northern Phalarope *Lobipes lobatus.*

Recorded in groups of three and eight, 175 miles west of Tampa, Florida, on March 4, 1918 (Helmuth 1920, p. 258). Two were seen at Aransas Refuge, Texas, April 4, 1940, and seven on April 25.

Pomarine Jaeger *Stercorarius pomarinus.*

The relative status of the three species of jaegers in the Gulf is a somewhat uncertain matter, since they are difficult to distinguish in life even at close range and since most of the records are based upon sight identifications. No specimen of the pomarine jaeger has ever been taken in the Gulf proper, but a fair proportion of the sight identifications have been assigned to this species. There has been only one report from the western half of the Gulf, that of a single bird seen on Bolivar Peninsula, Texas, June 16 and 27, 1933 (Williams 1938, p. 68); but there are several records for the eastern half: various points at sea in March and April (Helmuth 1920, p. 261; Moore 1951, p. 13); one on September 17, 1950, 30 miles off Carabelle, Florida (Stoddard, in litt.); one on January 10, 1951, at sea 158 miles north of Progreso, Yucatán (Bullis, in litt.); and one on August 3, 1930, off Contoy Island, Quintana Roo. Jaegers seem to be a bit more common in the Straits of Florida and Cuban waters,where this species has been collected.

Parasitic Jaeger *Stercorarius parasiticus.*

Seemingly slightly commoner than the preceding species, especially to the north: not uncommon in Cuban waters; flocks of 10 to 15 reported by

Audubon on Florida Keys in April; specimen taken in Bay of Florida, April 26, 1903; seen at Palma Sola, Florida, November 5, 1909, and December 11, 1911; seen in northern Gulf in March and April (Moore 1951, p. 13); several seen 90 to 158 miles at sea north of Progreso, January 10 and 11, 1951 (Bullis, in litt.). Additional observations, by Lowery (unpublished notes), believed referable to the present species, are: one seen 28 miles south, and nine seen 56 miles south of Southwest Pass, Louisiana, on April 21, 1948; four seen near mid-Gulf on April 22; one seen 101 miles south of the Louisiana coast on May 2. There are no definite spring records after this date, though two probable parasitic jaegers were observed at Pensacola on June 17, 1951.

Long-tailed Jaeger *Stercorarius longicaudus.*

An arctic species ranging south in winter barely to the Gulf. The records are mostly from the extreme eastern part of the Gulf or its environs: one collected at Marco in the winter of 1884; one seen at Passage Key, Tampa Bay, on numerous dates between June 14 and 30, 1910, one noted on Matecumbe Key, February 27, 1929. In addition, the long-tailed jaeger has been reported from the northern part of the Gulf on March 9 and April 6 (Moore 1951, p. 14), and has been taken at Matanzas Bay, Cuba, on November 29.

Kittiwake *Rissa tridactyla.*

The only evidence for the occurrence of this oceanic gull in the Gulf itself is Audubon's indefinite record for the Florida Keys. There is, however, a January specimen from the vicinity of Havana, Cuba.

Sooty Tern *Sterna fuscata.*

Breeds widely on islands of the Gulf: Arcas Keys, Alacran Reef, and the Dry Tortugas. In addition, a female incubating an egg was noted on a little island outside of Tampa Bay, May 25, 1949 (Nicholson 1950, p. 71); two females that had an egg and behaved like a mated pair were collected in 1933 on Curlew Island, in the Chandeleur group off the coast of Louisiana; and a nest was reported June 5, 1938, in the Corpus Christi, Texas, area, where the species is said to have nested in numbers prior to 1895. The best known colony is that on the Dry Tortugas which has grown from an estimated 3,600 birds in 1903 to an estimated 120,000 birds in 1950 (Dilley 1950, p. 67). The birds generally arrive there in February and depart in September. Despite the size of this colony, there have been relatively few modern records from the Gulf mainland. In the past decade, for instance, the species has been reported there only six times: three occasions in August and September in the vicinity of Pensacola; June 26, 1949, in Bay County, Florida (Hallman, in litt.); October 4, 1949, at Cove, Texas; and near Port Isabel, Texas, May 6, 1948 (Cruickshank 1949, pp. 111–112). The Tortugas were the scene of a famous series of experiments with this species and the noddy tern by Watson and Lashley between 1907 and 1913, which demonstrated the great ability of the sooty tern to "home" but showed that this species cannot long remain in the water without drowning.

Bridled Tern *Sterna anaethetus.*

A tropical tern breeding as near to the Gulf as Cayo Mono Grande, Cuba. Half the Gulf records (Sprunt, 1951a, p. 59, 1951b, p. 223) are near the Florida Keys or the Dry Tortugas: one banded in the Bay of Florida, October 2, 1940; one taken at the Marquesas Keys, July 9, 1938; one seen at New Ground Shoal, 25 miles east of the Dry Tortugas, June 21, 1946; one taken at Fort Jefferson, September 7, 1949. The species has also been reported 90 miles west of Tampa, date unspecified (Packard, 1947, p. 131); at Alligator Point, Florida, August 31, 1950 (a count of six); at Pensacola, Florida, December 29, 1945 (specimen preserved); and 10 miles south of Foley, Alabama, September 2, 1932, when six birds were seen (Edwards, 1933, p. 105).

Noddy Tern *Anöus stolidus.*

Breeds on Contoy Island and on the Dry Tortugas, where it has arrived at least as early as March 26. The Tortugas colony has variously accommodated from 400 (in 1903) to 622 (in 1950) birds (Dilley 1950, p. 68). Most of the fishing of this species is said to be done within about 10 miles of the island. Consequently, the noddy tern is less often seen from the mainland even than the sooty tern. We know of only two records in this century of its occurrence on the Gulf coast: a few seen in Tampa Bay in July 1923; one collected August 30, 1942, at Sabine Wildlife Refuge, Louisiana (Atwood, 1943, pp. 454–455). However, four

were seen 90 miles west of Tampa after a hurricane sitting on a floating log (Packard, loc. cit.). The noddy is a much better swimmer than the sooty tern.

Dovekie *Plautus alle*

A far northern species and the only representative of the family Alcidae ever known to have reached the Gulf. In 1932, during a tremendous southward influx of dovekies apparently unprecedented within the historic period (see Murphy and Vogt, 1933, pp. 322–333), birds reached Matecumbe Key, Florida, on December 3 and 9; Matanzas Bay, Cuba, on November 9; and Santa Maria del Rosario, 20 kilometers from Havana, on December 1 and 6. Since that year it has been reported at least three times: one observed at Key West in the winter of 1936–37 (Longstreet, 1937, p. 66); one collected at St. Andrews Bay, Florida, December 7, 1939 (Stevenson, 1950, p. 612); several seen and one taken at Key West, December 10, 1950; and another captured and released by J. R. De Weese, at Dry Tortugas in early December 1950.

II. BIRDS OF THE COAST

As one moves shoreward from the open Gulf, the scene changes from one of wide vistas of seemingly empty sea and sky to one with a bird life of bewildering abundance and variety. In 5 minutes on the coast one can frequently see a greater number of kinds of birds than is listed in the whole pelagic category. In December 1950, a 1-day bird count made within a circle 15 miles in diameter, reaching back from the Gulf coast at Cameron, Louisiana (Newman and party, 1951) disclosed the presence of no less than 142 species. Fully nine-tenths of the species of birds in eastern North America have been recorded at one time or another in the counties bordering the Gulf coasts of Florida, Alabama, Mississippi, Louisiana, or Texas, and it is likely that all but a few of these species have occurred at certain times and places within a hundred yards of the surf. Except at the tip of the Florida Peninsula, these counties all lie within the Lower Austral Life-zone or its arid division, the Lower Sonoran. As one continues the circuit of the Gulf coast, however, one passes into the Tropical Region and through two sharply differentiated faunas, that of Mexico and that of the West Indies. These places are so rich in birds of their own that the avifauna of the narrow coastal strip extending back a few hundred yards from the Gulf beach along its entire periphery very probably exceeds the entire avifauna of the United States in variety.

Which of these birds are to be considered coastal birds? As to their separation from the birds of the open Gulf, a line of distinction has already been laid down. The coastal birds may be said to be those species that occur more frequently on the shores of the mainland than on the open sea. This definition works very well except as it applies to a quartet of water birds that are more commonly encountered on the coastal islands of the Gulf than on its mainland shores. The great white heron, which many believe to be nothing more than a color phase of *Ardea herodias*, is best known as a bird of the Florida Keys; but, though infrequently observed on the Florida Peninsula itself, it has at least nested there. The man-o'-war-bird, popularly thought of as a bird of the oceans, has its center of abundance in the Gulf at roosting grounds on the islands near the coast; but, though it could have been classed with the offshore birds as here defined, it wanders often enough to the edges of the mainland to qualify as a borderline case. The oyster-catcher is so wary of man that it now spends most of its time on the inshore islands rather than the peripheral shores; but it remains clearly a littoral species. And the roseate tern, which has established a breeding colony in the Dry Tortugas, is as infrequently reported on the coasts of the mainland as some pelagics, but this is doubtless due to its small numbers, the difficulty in distinguishing it, and its scattered distribution when not nesting.

The problem of delimiting the coastal species from the inland bird fauna is much more complex. Such delimitation cannot be accomplished by simply considering the occurrence of a given species in a given place. As a starting point, we may specify that to qualify as a true part of the Gulf avifauna a coastal bird must be a species of the intertidal zone. But just what is meant by "a species of the intertidal zone?" If we interpret it to mean an organism confined to the area between the low-tide mark and the high-tide mark, virtually no species in this highly mobile class of animals with which we are dealing fits the definition. If on the other hand, we interpret it as any organism present at times in the inter-

tidal zone but also occurring elsewhere, we must admit an impossibly large part of the avifauna of the United States, Mexico, and Cuba. Tree growth invades the intertidal zone through the medium of the mangroves, forming the physical basis of a community over the very waters of the Gulf, where a whole host of small land birds must occur as visitants, though their identities remain uncertain since the situation has never been analyzed from that point of view, even in the United States. Even where there are no mangroves, the problem remains. Starlings, as one example, sometimes descend into the intertidal zone in such numbers that they blacken the beaches. But to consider the starling a Gulf bird is to accept a criterion of inclusion that has no practicable limit. Nor can the difficulty be satisfactorily avoided by setting up taxonomic distinctions so as to exclude all species not of the lower orders commonly called water birds. Some passerine birds, such as the seaside sparrow are so strictly Gulf birds that they have developed subspecies virtually endemic to its littoral. Conversely, some birds that are shorebirds by virtue of their systematic position, such as the upland sandpiper, almost never set foot on earth dampened by salt water.

From the ecological point of view, the birds found on the coast form a continuous gradient from species apparently dependent for their existence on some factor associated with salt water to species that enter the intertidal zone only as intruders. Whether or not they are physiologically capable of doing so, such birds as the brown pelican, the oyster-catcher, Cabot tern, and seaside sparrow seldom venture out of sight of salt water. Some races of the clapper rail, long-billed marsh wren, and sharp-tailed sparrow seem equally bound to salt water; but the species include other races adapted to a life inland. The laughing gull, gull-billed tern, and black skimmer, though mainly birds of the intertidal zone, prove their ability to exist away from it by occasional appearances in the interior. Several kinds of shorebirds, including the red knot, sanderling, and marbled godwit, are almost never found outside the zone of tidewater in the region of the Gulf of Mexico, yet have breeding grounds in interior situations of the northern United States or Canada. The white-faced ibis, the snow and blue geese, the dowitcher, and the Wilson phalarope, among others, occur chiefly in the immediate environs of the coast without being notably characteristic of salt water situations. Numerous species, for example, the horned grebe, the greater scaup duck, both yellowlegs, the herring gull, and the least tern, are commonest on the coast but well represented inland. Contrariwise, the black-crowned night heron, the lesser scaup duck, the American coot, and the spotted sandpiper are well represented on the coast but commonest inland. The birds of the last two categories, together with a host of others that seem to be about equally well represented in both situations, are ecologically linked to aquatic food sources but not especially to salt water sources. It is questionable whether from a strictly objective point of view such species qualify any better as coastal birds than upland species that sometimes derive sustenance from food sources associated with the Gulf. Among such upland species may be mentioned the horned lark and the water pipit, which often feed at the very edge of the surf; the common goldfinch which resorts regularly to the outer beaches attracted by the ripening seeds of the sea oat, *Uniola paniculata;* and even the peregrine falcon which at seasons shows a preference for a diet consisting of birds of the littoral. Finally, living within sound of the surf, occur a host of birds whose ecological associations are essentially nonlittoral. On the narrow wooded ridges of coastal Louisiana, for example, that rise out of the marshes sometimes within a hundred yards of Gulf waters, are to be found breeding such species as the downy woodpecker, crested flycatcher, mockingbird, white-eyed vireo, orchard oriole, and cardinal.

To complicate matters further, the degree of association of various birds with salt water varies in different sections of the Gulf littoral. Along the northern part of the Yucatán Peninsula, where there are practically no inland water features, the water birds represented necessarily occur almost exclusively in the salt lagoons of the coast, even though many of them, including the pied-billed grebe, white ibis, and sora, are elsewhere primarily inhabitants of fresh water situations. Somewhat similar conditions obtain along the Texas coast where great migratory flocks of water birds are apparently channeled down a narrow flight lane that brings many fresh water species to the very edge of the Gulf. In the great

duck marshes of southern Louisiana, adjoining the Gulf, hunting pressure often causes surprising numbers of dabbling or pond ducks to seek an unaccustomed refuge beyond the surf.

The more one analyzes the avifauna of the coastal strip, the more futile it seems to try to set up an objective criterion to separate Gulf birds from non-Gulf birds. But it would be just as futile, even if space permitted, to attempt a complete résumé of all the birds occurring on the coast. The Gulf of Mexico simply does not provide a convenient natural bond for tying together major elements of the diverse avifaunas of the West Indies, the United States, and Mexico. Though many of the birds of the coast are closely linked to the Gulf ecologically, their practical associations from a reference standpoint are with the birds of the mainland, and information concerning their status is best sought in works dealing with the birds of the States and counties bordering the Gulf. Works of this nature, either published or in the course of publication, are listed in the section "Literature Cited," since they constitute the major sources from which material for this chapter has been drawn.

Since the present list of coastal birds is not offered as an exhaustive reference, it is not too critical a matter just how much it includes. We would formally define coastal species as those that characteristically occur over the inshore waters within sight of the mainland and over that part of the mainland itself washed by tides. The term "characteristically," however, permits a wide latitude of interpretation and in applying it, we do not pretend to have exercised strict consistency. Many readers will doubtless think of birds they would consider more deserving of a place in the account than some species we have admitted. All we have tried to do is to give a comprehensive list of those birds that are definitely commoner in salt water than elsewhere, together with a somewhat arbitrary sampling of other species occurring on the coast but not primarily birds of the littoral.

Even on this selective basis, the coastal avifauna is a large one, amounting to 125 species. The relationships of these birds with the Gulf have many aspects—their relative abundance on the different coasts, their relative abundance at different seasons, their status as breeders or visitants, their degree of association with salt water. Since, over the vast geographical extent of the Gulf, the seasons of many species vary from place to place, the complete status of a coastal bird is often a very complicated matter. In order to convey as much information as possible in the smallest space, we have presented the summary of coastal species in telegraphic form, arranged under three headings. The subdivisions are (1) Breeding Birds, (2) Regular Visitants, and (3) Species Not of Regular Annual Occurrence. If a species is present somewhere on the Gulf every year, it is deemed of regular annual occurrence. Records for 4 out of the past 10 years are regarded as good presumptive evidence of such yearly presence.

The ranges, for the most part, have been expressed in terms of their extent counterclockwise around the Gulf perimeter, starting with Cuba or Florida, at the open end of the Gulf. The phrase "Florida to Texas," for example, is meant to imply that the species concerned is represented on the coasts of both Florida and Texas, as well as on the coast in between. As an indication of the extent to which the various species frequent the coast, we have employed before the name of each, one, two, or three asterisks. Three asterisks (***) denote a species that is seldom seen away from the coast; two asterisks (**), a species that is not infrequently found inland, but which is consistently equally common, or more common, on the coast; one asterisk (*), a species that is usually more frequent inland, but which for brief periods may be equally common on the coast. Our decisions in this matter have been based mainly upon the distribution of these birds in the States, Territories, and Provinces bordering on the Gulf, with recourse to a broader ecological viewpoint only in the case of those rare visitants that do not otherwise provide a basis of comparison. The resulting classification is a very rough one and one resting to some extent on personal opinion, since all the difficulties encountered in defining a coastal category are compounded when one attempts to divide that category into parts.

The brief statements as to the relative abundance of the different species along the different sections of the coast, of course, merely reflect the incidence of the currently available records and not necessarily the true incidence of the birds themselves. Some sections of the Gulf coast

have been studied much more intensively than others. Indeed, there are vast stretches of the Gulf coast, such as in Mexico, where the littoral birds have been almost entirely ignored. There are shorebirds, for example, which are known to be regularly abundant on the coast of Texas but for which there are no records at all for adjacent Tamaulipas. Therefore, conclusions based on relative abundance as indicated in the following outline should be formulated with caution.

COASTAL BREEDING BIRDS

**White Pelican, *Pelecanus erythrorhynchos*.—Irregular breeder in Texas; winter visitant to all coasts, most abundant from Florida to Texas, a mere straggler in Cuba.

***Brown Pelican, *Pelecanus occidentalis*.—Abundant resident throughout.

**Double-crested Cormorant, *Phalacrocorax auritus*.—Common (Cuba and Florida) to rare and irregular (Texas) summer resident or breeder; common visitant to Quintana Roo.

**Olivaceous Cormorant, *Phalacrocorax olivaceus*.—Fairly common to abundant resident from Louisiana counterclockwise to Cuba.

***Man-o'-war-bird, *Fregata magnificens*.—Occurs in colonies at Tamiahua Lagoon, Veracruz, on Contoy Island, and in Cuba; one report of nesting in Texas; abundant visitant, mainly April to October, to coastal islands all around Gulf, infrequently appearing over the inshore waters.

***Great White Heron, *Ardea occidentalis*.—Resident in Cuba (sparingly) and on Florida Keys (in fair numbers); extremely rare visitant to Mississippi, Texas, and Yucatán.

**Great Blue Heron, *Ardea herodias*.—Common resident and breeder from Cuba to Texas; common winter visitor on all coasts.

**American Egret, *Casmerodias albus*.—Common resident throughout, less numerous in winter on northern coast.

**Snowy Egret, *Leucophoyx thula*.—Status essentially the same as that of preceding species.

***Reddish Egret, *Dichromanassa rufescens*.—Uncommon to locally common breeder from Texas counterclockwise to southern Florida; rare to uncommon visitant from northwest Florida to Louisiana, extremely rare in winter.

**Louisiana Heron, *Hydranassa tricolor*.—Abundant summer resident throughout; uncommon in midwinter on northern coast.

*Little Blue Heron, *Florida caerulea*.—Fairly common to abundant throughout; uncommon to rare in midwinter on the northern coast.

**Black-crowned Night Heron, *Nycticorax nycticorax*.—Breeds from Cuba counterclockwise to Veracruz but common as a breeder only in Florida; more plentiful after the nesting season.

*American Bittern, *Botaurus lentiginosus*.—Breeds occasionally in Florida and Louisiana; fairly common winter visitant to all coasts.

**Least Bittern, *Ixobrychus exilis*.—Uncommon to locally common resident, recorded from all coasts; extremely rare on Gulf coast of United States in winter.

Boat-billed Heron, *Cochlearius cochlearius*.—Resident from Tamaulipas to Yucatán, but relative abundance in tidewater uncertain.

*Wood Ibis, *Mycteria americana*.—Mainly a fall transient and summer resident (not certainly known to breed) from northwestern Florida to Texas; locally common resident on the more southern coasts.

**White-faced Ibis, *Plegadis mexicana*.—Resident from Louisiana to Veracruz, but less numerous in winter in northern part of range.

**Roseate Spoonbill, *Ajaia ajaja*.—Increasingly numerous resident, at least locally, from southwestern Louisiana counterclockwise to southern Florida; rare or absent from northwest Florida to central Louisiana, especially in winter.

***Flamingo, *Phoenicopterus ruber*.—Breeds in Yucatán and Cuba; winter visitant to Campeche; occasional visitant to Florida, Texas, and (formerly) the intervening coast.

**Mottled Duck, *Anas fulvigula*.—Fairly common resident from Florida west to Texas, unrecorded as a breeder between central Florida and Louisiana.

*Blue-winged Teal, *Anas discors*.—Uncommon local breeder in Louisiana and Texas; winter visitant to all coasts; most common from September to April.

**Bald Eagle, *Haliaeetus leucocephalus*.—Breeds from Florida (in numbers) to Texas (less numerously); rare from May to August.

**Osprey, *Pandion haliaetus*.—Breeds in Yucatán, and from Florida to Texas; occurs in migration on all coasts; extremely rare on northern Gulf coast in December and January.

***Clapper Rail, *Rallus longirostris*.—Abundant and sedentary resident from Yucatán counterclockwise to Texas.

***Rufous-necked Wood Rail, *Aramides axillaris*.—Resident in coastal lagoons of Yucatán.

***Black Rail, *Laterallus jamaicensis*.—Known to nest rarely in Florida; casually recorded in migration or as winter visitant in Cuba, Louisiana, and Texas; not reported in January or February or from June to August.

*American Coot, *Fulica americana*.—Local breeder in small numbers from Cuba counterclockwise to Texas; recorded in June in Veracruz; visitant to all coasts, mainly October to April.

***American Oyster-catcher, *Haematopus palliatus*.—Uncommon local breeder, definitely known to nest only in Florida, Louisiana, and Texas, but also recorded from Tamaulipas, Veracruz, Yucatán, and Cuba.

Coastal Breeding Birds—Continued

**Snowy Plover, *Charadrius alexandrinus.*—Resident in small numbers from Cuba counterclockwise to Mississippi and in Texas; winter visitant in Louisiana; in general most common in migration when also recorded in Yucatán.

***Wilson Plover, *Charadrius wilsonia.*—Common summer resident from Cuba counterclockwise at least to Texas, breeding also in Veracruz; visitant to Yucatán.

**Azara Plover, *Charadrius collaris.*—Fairly common summer resident in Veracruz, recorded also in Tabasco.

**Long-billed Curlew, *Numenius americanus.*—Fairly common breeder in Texas; abundant there in winter, when also fairly common from Louisiana to Yucatán; rare winter visitant east to Florida and Cuba.

***Willet, *Catoptrophorus semipalmatus.*—Breeds from Florida counterclockwise to Tamaulipas; common (summer) to fairly common (winter) resident where it breeds; visitant to Veracruz, Yucatán, and Cuba.

**Avocet, *Recurvirostra americana.*—Rare breeder and winter resident, common transient, in Texas; occurring at least as rare to uncommon visitant from Cuba counterclockwise to Veracruz.

**Black-necked Stilt, *Himantopus mexicanus.*—Locally common summer resident in Cuba and Florida peninsula and from Louisiana to Yucatán; rare from November to February in Louisiana and Texas.

***Laughing Gull, *Larus atricilla.*—Common summer resident on all coasts but not actually found nesting from Tamaulipas to Tabasco; somewhat less common in winter, at least in United States and Cuba.

***Gull-billed Tern, *Gelochelidon nilotica.*—Breeds from northwest Florida to Texas; fairly common in breeding range from March to September, rarer in other months; visitant to Cuba and Veracruz.

**Forster Tern, *Sterna forsteri.*—Breeds in Louisiana and Texas and most numerous there from March to December; visitant as far as Florida and Veracruz.

***Common Tern, *Sterna hirundo.*—Known to breed only on Dry Tortugas but visitant throughout in fall, winter, and spring.

***Roseate Tern, *Sterna dougallii.*—Nests irregularly on the Dry Tortugas (none to 200 pairs); an extremely rare visitant around the coast to Texas and a rare visitant to Cuba; recorded from January to May and in July, September, and November.

**Least Tern, *Sterna antillarum.*—Breeds from Yucatán counterclockwise to Texas; common only from April to October.

***Royal Tern, *Thalasseus maximus.*—Common throughout, but not now known to nest from Florida to Mississippi or from Tamaulipas to Campeche.

***Cabot Tern, *Thalasseus sandvicensis.*—Fairly common at some season on virtually all coasts, but not now known to breed from Cuba to Mississippi or from Tamaulipas to Campeche; rare in winter on northern Gulf coast and in southern Texas, uncommon in peninsular Florida in summer.

**Caspian Tern, *Hydroprogne caspia.*—Common breeder and resident in Louisiana and Texas; visitant as far as Cuba and Yucatán.

***Black Skimmer, *Rynchops nigra.*—Breeder and resident in varying numbers from Florida counterclockwise to Yucatán; less common in winter on northern coast; casual in Cuba.

**Mangrove Cuckoo, *Coccyzus minor.*—Breeds from Tamaulipas counterclockwise to southern Florida; uncommon summer resident in Florida, March to September; resident, but possibly not characteristic of coast, elsewhere.

***Gray Kingbird, *Tyrannus dominicensis.*—Summer resident from Cuba to southern Florida (where common) to Alabama (one record), mainly from April to September but unrecorded only in November.

**Long-billed Marsh Wren, *Telmatodytes palustris.*—Abundant to locally uncommon resident from Florida west to Texas, occurring south in winter at least to Veracruz.

**Mangrove Swallow, *Iridoprocne albilinea.*—Resident from southern Tamaulipas to Yucatán.

***Black-whiskered Vireo, *Vireo calidris.*—Summer resident from Cuba to Anclote Key, Florida, mainly from April to September but also recorded in March and October.

***Mangrove Warbler, *Dendroica petechia.*—Coastal races from Tamaulipas counterclockwise to Florida Keys; seasonal status uncertain.

**Red Wing, *Agelaius phoeniceus.*—Common resident throughout, abundant in winter.

**Boat-tailed Grackle, *Cassidix mexicanus.*—Abundant resident from Florida to Yucatán.

***Seaside Sparrow, *Ammospiza maritima.*—Locally abundant resident from Florida west to Texas.

***Cape Sable Sparrow, *Ammospiza mirabilis.*—Presumed to be resident at Cape Sable (at least formerly) and in Collier County, Florida, but definitely recorded only in February, April, and May.

REGULAR VISITANTS ON THE COAST

**Common Loon, *Gavia immer.*—Florida west to Texas in moderate to large numbers, mainly from October to May.

**Horned Grebe, *Colymbus auritus.*—Florida (common in the northern part) to Texas (where uncommon); mainly November to April, but unrecorded only from June to September.

**Eared Grebe, *Colymbus nigricollis.*—Rare to not uncommon from Texas south to Veracruz, October to April and occasionally May; unrecorded from June to September.

**Canada Goose, *Branta canadensis.*—Florida counterclockwise to Veracruz; common in United States part of range (except peninsular Florida); mainly October to March, but unrecorded only in August.

Regular Visitants on the Coast—Continued

*White-fronted Goose, *Anser albifrons.*—Visitant rarely to Cuba and Florida and regularly from Louisiana (where fairly common) and Texas (where abundant) to Veracruz; September to April only.

**Snow Goose, *Chen hyperborea.*—Cuba counterclockwise to Texas; abundant in Louisiana and Texas, decreasingly common to the east; mainly October to March.

**Blue Goose, *Chen caerulescens.*—Cuba counterclockwise to Texas; rare to uncommon in the east, abundant in the west; mainly October to May, but several hundred said to have summered in Louisiana in 1949.

**Black Duck, *Anas rubripes.*—Cuba (doubtfully) and Florida to Texas; mainly October to May, but unrecorded only in July and August.

*Shoveler, *Spatula clypeata.*—Visitant throughout, moderately common (eastern part) to common (western part) on United States Gulf coast; mainly October to April, but unrecorded only in July.

**Redhead, *Aythya americana.*—Visitant from Cuba to Tamaulipas; rare to uncommon except in Texas, where abundant; mainly October to May, but unrecorded only in August.

**Ring-necked Duck, *Aythya collaris.*—On all coasts, but apparently common only in Florida, and Louisiana; October (occasionally September) to April only.

**Canvasback, *Aythya valisineria.*—Cuba counterclockwise to Veracruz; rare (Cuba) to moderately common (Louisiana); mainly October to May, but unrecorded only in August.

**Greater Scaup Duck, *Aythya marila.*—Cuba (allegedly) and Florida west to Texas, but relative abundance uncertain; mainly November to March, but unrecorded only from June to October.

**Lesser Scaup Duck, *Aythya affinis.*—Common on all coasts; mainly October to May.

**American Goldeneye, *Bucephala clangula.*—In small numbers from Florida counterclockwise to Texas; mainly December to March, but unrecorded only from June to October.

**Bufflehead, *Bucephala albeola.*—Rare to uncommon from Cuba (where only once recorded) counterclockwise to Tamaulipas; mainly November to March, but unrecorded only from June to September.

**Oldsquaw, *Clangula hyemalis.*—Rare to uncommon from Florida to Texas; November to May only.

**American Merganser, *Mergus merganser.*—Uncommon from Florida counterclockwise to Tamaulipas; mainly November to April, but unrecorded only from July to September.

**Red-breasted Merganser, *Mergus serrator.*—Casual in Cuba, fairly common to abundant from Florida to Texas; mainly November to May.

*Virginia Rail, *Rallus limicola.*—Not commonly observed but recorded on all coasts; mainly October to April.

*Sora, *Porzana carolina.*—Common transient and fairly common winter visitant, recorded on all coasts and in every month.

***Piping Plover, *Charadrius melodus.*—Winter visitant, rare in Cuba, fairly common from Florida west to Texas; recorded in every month, but infrequent in summer.

**Ringed Plover, *Charadrius hiaticula.*—On all coasts; most abundant in April and May and in August and September.

*Mountain Plover, *Eupoda montana.*—Rare to abundant spring migrant (March to May) and rare fall migrant and winter visitant in Texas; once recorded (in December) at Key West, Fla.

*Golden Plover, *Pluvialis dominicus.*—Spring migrant in March and April, rare in Cuba, regular from northwest Florida to Texas; occasional on northern Gulf coast in fall and winter.

**Black-bellied Plover, *Squatarola squatarola.*—Common migrant and winter visitant throughout, less common in summer.

***Ruddy Turnstone, *Arenaria interpres.*—Fairly common to abundant on all coasts; most numerous in spring and fall.

***Hudsonian Curlew, *Numenius phaeopus.*—Recorded from Cuba counterclockwise to Tabasco, but common only in Florida, Louisiana, and Texas, and there only as a migrant; irregular in winter and autumn.

*Spotted Sandpiper, *Actitis macularia.*—On all coasts; most common in April and May and from August to November; uncommon on northern coast in winter; doubtfully recorded nesting near coast in Louisiana and Texas.

**Greater Yellow-legs, *Totanus melanoleucus.*—Common to abundant on all coasts in spring and fall, fairly common in winter.

**Lesser Yellow-legs, *Totanus flavipes.*—Status similar to that of preceding species.

***Red Knot, *Calidris canutus.*—Recorded from Florida to Texas and in Veracruz and Yucatán; apparently really common only in peninsular Florida, where it is an abundant spring and fall transient.

**Pectoral Sandpiper, *Erolia melanotos.*—Common migrant, recorded from Cuba counterclockwise to Veracruz; mainly March to April and July to October; rare and irregular in winter, unreported in June.

***White-rumped Sandpiper, *Erolia fuscicollis.*—Recorded on all coasts, but really common only in Texas; mainly late April to June and August to October, but also recorded in December and February.

**Least Sandpiper, *Erolia minutilla.*—Common to abundant migrant and fairly common winter visitant on all coasts.

***Red-backed Sandpiper, *Erolia alpina.*—Common to abundant from Florida west to Texas; mainly October to May.

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Regular Visitants on the Coast—Continued

**Dowitcher, *Limnodromus griseus*.—Common winter visitant and abundant spring and fall transient on all coasts except in Cuba (where uncommon); most numerous from August to October and March to early May.

**Stilt Sandpiper, *Micropalama himantopus*.—Cuba counterclockwise to Veracruz, but fairly numerous only in northwestern quadrant and in Cuba; mainly April to May and July to October, but unrecorded only in January and February.

**Semipalmated Sandpiper, *Ereunetes pusillus*.—Common to abundant on all coasts, except from Tamaulipas to Tabasco; least numerous in summer.

**Western Sandpiper, *Ereunetes mauri*.—Common to abundant winter visitant and transient from Florida west to Texas; infrequently recorded in Cuba and Veracruz; uncommon on all coasts in summer.

***Marbled Godwit, *Limosa fedoa*.—On all coasts; common to abundant in Florida and Texas, but rare to uncommon elsewhere; mainly July to April.

***Sanderling, *Crocethia alba*.—Common to abundant on all coasts; least numerous in early summer.

**Herring Gull, *Larus argentatus*.—Recorded on all coasts, occurring mainly October to March and mainly around northern half of Gulf, where abundant.

***California Gull, *Larus californianus*.—Winter visitant, recorded only from Texas and Veracruz and from October to June.

**Ring-billed Gull, *Larus delawarensis*.—Fairly common to common from Cuba counterclockwise to Texas, mainly October to April.

**Franklin Gull, *Larus pipixcan*.—Florida and Louisiana to Yucatán, but recorded as abundant only in Texas, in April and from September to December; no records for July or August.

**Bonaparte Gull, *Larus philadelphia*.—Cuba to Texas, common except in Cuba, southern Florida, and south Texas; mainly November to April, but unrecorded only in July.

**Black Tern, *Chlidonias niger*.—Common transient on all coasts, except in Cuba, where rare; mainly April to June and July to October, but also in November and December.

**Sharp-tailed Sparrow, *Ammospiza caudacuta*.—Florida west to Texas; common except in south Florida; mainly October to March, but unrecorded only from June to August.

VISITANTS TO COAST NOT OF REGULAR ANNUAL OCCURRENCE

***Red-throated Loon, *Gavia stellata*.—Several old, and one recent, record from Florida (Hillsboro, November 23, 1949); four recent records from Texas (Galveston Bay region, November 27–March 21).

***Holboell Grebe, *Colymbus grisegena*.—Several sight records, most of them recent, from Florida and from Rockport, Tex.; extreme dates: November to March.

**Western Grebe, *Aechmophorus occidentalis*.—Two records at Rockport, Tex., one bird on December 12, 1936, and four on February 2 and 4, 1949; also one seen at Pensacola, November 12, 1927.

***Whistling Swan, *Cygnus columbianus*.—Several records, mostly November to March and most frequently from northwest Florida, but including Louisiana and Texas; formerly more numerous.

***Trumpeter Swan, *Cygnus buccinator*.—Several records, Louisiana, Texas, and Tamaulipas, but all prior to 1916.

***American Brant, *Branta bernicla*.—Two old records from Florida; also reported from vicinity of Rockport, Texas, in 1910, 1938 (five on October 5 and 19; two on November 8) and 1950 (one on April 22).

**Ross's Goose, *Chen rossii*.—Twice taken in Louisiana (1910 and 1916); twice observed at Cove, Texas, in 1948 and November 22, 1950.

***Harlequin Duck, *Histrionicus histrionicus*.—Two seen on January 14, 1945, near Rockport, Texas, and one on January 29 at Aransas Refuge; also single old records for Florida and Louisiana.

***Surf-bird, *Aphriza virgata*.—One seen at Port Aransas (April 1–12, 1951).

**Eskimo Curlew, *Numenius borealis*.—Two reported from Galveston Island, Texas, April 29, 1945; not otherwise recorded from the Gulf coast in over 50 years.

***Purple Sandpiper, *Erolia maritima*.—One collected at Marco, Florida, November 1886; five seen at St. Joseph Bay, Florida, May 29, 1948 (Hallman *in litt.*)

***Sharp-tailed Sandpiper, *Erolia acuminata*.—One reported at Galveston, Texas, March 21, 1948.

***Curlew Sandpiper, *Erolia ferruginea*.—One seen April 13, 1947, Galveston Island, Texas.

***Glaucous Gull, *Larus hyperboreus*.—Several records, Florida, Mississippi, and Texas; December 22 to May 10.

***Iceland Gull, *Larus leucopterus*.—One taken at Crystal River, Florida, February 9, 1927, and another photographed from the Long Key viaduct, Florida, January 6, 1950 (Cruickshank, 1951: 113).

***Great Black-backed Gull, *Larus marinus*.—One seen at Rockport, Texas, February 21–27, 1949; two old and indefinite Florida records, as well as two immature birds seen on Matecumbe Key, Florida, February 4, 1935 (Broun, 1935: 320).

***Lesser Black-backed Gull, *Larus fuscus*.—One reported at Key West, Florida, March 10, 1938.

***Black-headed Gull, *Larus ridibundus*.—One seen at Tampa Bay, Florida, March 2, 1948 (Cruickshank, 1949: 205); one taken in Bay of Campeche near Veracruz, February 1912.

Visitants to Coast Not of Regular Annual Occurrence—Continued

***Sabine Gull, *Xema sabini*.—One taken at Corpus Christi, Texas, October 4, 1889; one seen on Padre Island, Texas, December 30, 1951.

***Elegant Tern, *Thalasseus elegans*.—One taken at Corpus Christi, Texas, July 25, 1889.

Despite the great geographic extent of the Gulf of Mexico, only one species of bird is endemic to its shores or to its islands, in the sense that it occurs there and nowhere else. This is the Cape Sable sparrow, a bird so closely related to *Ammospiza maritima* that some taxonomists would prefer to place it under that species. However, at least 16 subspecies peculiar to the Gulf area are rather generally recognized. While the present summary deals primarily with the status of birds as species, these endemic races are a subject of considerable pertinence, since they reveal the effectiveness of the Gulf perimeter in the development of geographic variations. Of these subspecies restricted to the Gulf coast, four are seaside sparrows: *Ammospiza maritima peninsulae*, occurring from Tampa Bay to Lafayette County, Florida; *A. m. juncicola*, from Taylor County to St. Andrew Bay, Florida; *A. m. fisheri*, from the coast of Alabama to High Island, Texas; and *A. m. sennetti*, from Galveston Bay at least to Corpus Christi, Texas. Three are clapper rails: *Rallus longirostris insularum*, of the Florida Keys; *R. l. saturatus*, of the coasts from Alabama west at least to Rockport, Texas; and *R. l. pallidus*, of the northeastern coast of the Yucatán Peninsula. Two are long-billed marsh wrens: *Telmatodytes palustris marianae*, occurring from Charlotte Harbor, Florida, to Mobile, Alabama; and *T. p. thryophilus*, of the coasts of Mississippi, Louisiana, and Texas. The remaining endemics with their respective ranges are: the nominate race of the great white heron, *Ardea occidentalis occidentalis*, southern Florida and the Florida Keys; a reddish egret, *Dichromanassa rufescens colorata*, the coast of the Yucatán Peninsula and its offshore islands; an insect hawk, *Buteo magnirostris gracilis*, islands off the northwestern coast of the Yucatán Peninsula; a barn swallow, *Hirundo rustica insularis*, coastal islands and beaches from northwestern Florida to southeastern Louisiana; a horned lark, *Eremophila alpestris giraudi*, southwestern Louisiana to northern Tamaulipas; a Carolina wren, *Thryothorus ludovicianus burleighi*, islands off the Mississippi coast; and a red-wing, *Agelaius phoeniceus littoralis*, Choctawatchee Bay, Florida, to Galveston, Texas.

A striking feature of the coastal bird list is, however, that it includes only three species that have never been recorded in the United States. Many a person interested in birds tends to think of tropic shores as places teeming with strange and unfamiliar species; but to the extent that this expectation is realized around the southern half of the Gulf, it is mainly fulfilled by those resident land birds whose home ranges happen to adjoin tidewater or to encroach upon it. The birds of the lower orders, the water birds that necessarily make up the great bulk of any coastal avifauna in the strict sense, are for the most part species of ancient origin that have extended their ranges over vast areas of the hemisphere and the world. The tropical water birds that have occurred in the lands bordering the Gulf but have never reached the United States are, with the exception of the three named in the summary and one accidental, all primarily inland species, at least insofar as available records reflect their distribution. The group is a rather small one, consisting of eight rails, four ducks, four herons, two sun-grebes, two shorebirds, a stork, and a tern. Twenty-nine species in the summary have yet to be reported from the southern half of the Gulf, but well over half of them are not of regular annual occurrence. If we were to divide the Gulf into an eastern and a western half by a line passing between Louisiana and Mississippi and along the western edge of the Yucatán Peninsula, that is, approximately by the 90th meridian, we would find that only four of the listed breeders and regular visitants have never been observed on the shores west of the line, while only three have yet to be seen on the shores east of it. To put these facts in a different way, all but 19 of the birds in the groups of regular annual occurrence have occurred at times and places on the northern and southern, as well as the eastern and western, Gulf coast. The real coastal avifaunas of all sections thus have a tremendous common denominator, and their variance is more a matter of relative abundance of individuals of

species rather than the mere presence or absence of particular species.

The wide geographical ranges of many coastal birds are related to the fact that they are highly migratory. A vast majority of the coastal species move, in part at least, southward in winter beyond the boundaries of the United States. In doing so, they are believed mainly to follow coastwise routes. Notable in this regard are the herons and shorebirds. It is a common sight to see flocks of each, in spring, flying in close formations just beyond the surf, as they pass northward and eastward along the Texas coast. On the eastern side of the continent, the coastwise flights inevitably involve eventual passage over wide expanses of open sea. While the path followed by many birds doubtless leads across the Straits of Florida and the Caribbean Sea, there is evidence that others pass well out over the Gulf itself. The occurrence of over 50 species of coastal birds, in several cases regularly, on the Dry Tortugas (Sprunt, 1951a, b) is evidence of over water flights of considerable length. There are, in addition, specific records of coastal birds having been seen on the open Gulf by ornithologists aboard ships. Helmuth (1920) saw three great blue herons approximately 100 miles off the Louisiana coast on March 29, 1918, and five Louisiana herons the following day about 180 miles off Alabama. Frazar (1881) noted the ruddy turnstone 30 miles beyond the mouth of the Mississippi River on April 2, 1881, and Lowery (1946) recorded a single great blue heron and seven long-billed curlews, in the spring of 1945, 19 and 34 miles respectively, off the same promontory. J. C. Howell (in Lowery, 1946) observed one green heron, two least bitterns, and a single red-backed sandpiper on May 4, 1945, when his ship was plying between two points, 121 and 179 miles off Louisiana. Bullis and Lincoln (1952) describe the capture aboard ship of a roseate spoonbill 38 miles off Louisiana, and Packard (1947) states, without giving a date, that he saw a wood ibis, among other species, at least 10 miles from land. A. H. Howell (1932) notes of the black rail that "a migrant was taken on a vessel, off Pensacola, March 10, 1885." That coastal birds of several kinds, notably gulls, terns, and ducks, forage out to sea is a well-known fact, but there are so few specific records out on the Gulf that we are unable to analyze at this time the frequency of such visitations in offshore waters or the distances involved.

In this connection, it should be pointed out that the greatest seabird colonies of the Gulf are on islands. The majority of them lie within sight of the mainland, but a few of the species we class as coastal resort in part to the remoter islands where they nest side by side with birds that we place in the offshore category. Thus the royal tern is said to breed on the Arcas Keys; the Cabot tern on Alacran Reef; and the laughing gull, in both places. On May 20, 1912, on Alacran Reef, Kennedy (1917) collected two specimens from a flock of 10 sandpipers, which he called "Baird's sandpiper (*Tringa fuscicollis*)." This record is repeated in the account of the Baird sandpiper in the Mexican Check List, but according to J. D. Macdonald (in litt.), of the British Museum, where the specimens now repose, actually refers to the white-rumped sandpiper. This is apparently the only published observation of a transient migrant on any of the offshore islands of the Campeche Bank.

Just as these birds, for the most part, have a wide geographic representation around the Gulf, so too do they have a wide seasonal representation there. Among the entries in our coastal list that are of regular annual occurrence, 56 have the status of breeders, 49 occur as winter visitants, and 8 are migrants not regularly represented in summer or winter. There are no summer visitants in the strict sense. In 77 cases—that is, in the case of every species for which the annotation does not explicitly state or definitely imply otherwise—actual Gulf records are available for every month of the year. Such gaps as do occur are predominantly in summer (24 in the period from June through August against 8 in the period from December through February), demonstrating that winter is the period of greater variety. This contrast gains increased force from the fact that several of the species found in every month of summer seem never to be continuously present throughout the season. It is not uncommon among shorebirds for the last of the northbound migrants to delay their departure until early June and for the first of the southbound migrants to return before July 31.

One factor in the seasonal spread of the records is the central position of the Gulf, and the essentially mild climate that goes with it. Only infre-

quently, and then only on the northern coast, do conditions of food or temperature place absolute physical limitations on the ability of a bird to survive there. This is especially true of the large and non-insectivorous species that make up the bulk of a coastal bird list. Year after year, as a result, Gulf localities go on making reports of birds "earlier than ever before" or "later than ever before," even in the comparatively well-worked sections of the United States. We may expect the present monthly gaps in the record of occurrence to diminish steadily.

As a further consequence of climate and position, the patterns of seasonal activity on the Gulf differ rather strikingly from the patterns for the United States as a whole. The regional editors of "Audubon Field Notes" for the Gulf States often find themselves handling half of their records of northward migration during the so-called Winter Season, from December 1 to March 31. In the stated period of spring migration, April 1 to May 30, they find the major nesting events of the year taking place. And by the time they reach the nominal nesting season, June 1 to August 15, they are already concerning themselves with the first effects of southward migration. This last, somewhat paradoxical situation stems from the fact that early southward migratory movement results in the North in invisible subtractions from large summer populations, while in the South those same invisible subtractions are translated into additions to the avifauna or accretions to populations that are at very low ebb.

III. LAND BIRDS OVER THE OPEN GULF

In the discussions up to this point, we have been concerned with birds that frequent the region of the Gulf of Mexico and its tidal reaches *because* of the Gulf: species that are attracted by some particular environmental advantage, or set of advantages, that they find there. Now we turn to a group of birds of opposite relationship, those that occur over this same part of the earth's surface *despite* the Gulf. They are the land birds and the inland water birds that from time to time and in varying numbers have been observed out over the open Gulf during the seasons of migration.

From the strictly ecological point of view, such birds are not birds of the Gulf at all. But, in a broad ornithological sense, their associations with the Gulf are of vastly greater importance than those of either the pelagic or the coastal birds. Interposed as the Gulf and its environs are between the summer and winter ranges of scores of highly migratory species, they furnish the most favored testing grounds in the world for theories of bird migration, particularly hypotheses regarding the effect of water barriers.

As specifically related to the Gulf of Mexico, there are two such hypotheses. One is that normal bird migration between South and Central America on the one hand and North America on the other takes place around the edges of the Gulf. According to this view, the records of nonpelagic birds over the open Gulf are of the same nature as records of similar species over the North Atlantic—they represent displaced birds. It has been pointed out that such records are few and that, whenever impressive numbers of individuals have been involved, the associated weather conditions have been such that they might have blown or otherwise shifted birds from overland routes. The most spectacular observations of migrants have been along the Texas coast, and most transient spring migrants have been noted more commonly either in Texas or in peninsular Florida than on the north central Gulf where the bulk of the trans-Gulf flights might be expected to land in spring, if they occur. Indirect evidences of trans-Gulf migration, such as comparative arrival dates in the United States, can be explained without assuming that any major migration routes lie across the Gulf. As originally expounded, these views were carefully confined to spring migration. More recently it has been implied that migrants do not customarily cross the Gulf in fall either.

The opposing hypothesis holds that, while large numbers of birds, particularly those that winter in Mexico, do migrate northward entirely overland, a significant proportion of those returning from South and Central America fly directly across the Gulf from Yucatán. It is pointed out that trans-Gulf migrations may be expected to take place on a very broad front with so much resultant dispersal that the number of birds observable at any one location should be small, and that the only concentrative factors operating on the Gulf are those associated with bad weather. In the light of these considerations, the present

records of small land birds over the Gulf are just the sort of records one should anticipate if trans-Gulf migration is an important reality. Because of the failure of recent fieldwork in eastern Mexico to produce more than a few scattered records of many migrants that are overwhelmingly abundant in Texas, the volume of the flight on the coast of Texas is regarded as evidence in favor of trans-Gulf migration, rather than evidence against it. Telescopic studies of the density and direction of night migrations leaving the coast of Yucatán have shown that the over-all trend of the flights is directed northwestward toward the Texas coast in conformity with the prevailing movement of the air masses in the western Gulf. And finally, these same studies have indicated that the flights are of major proportions.

This brief summary does not do full justice to the arguments supporting either hypothesis. It will serve, however, to indicate the main features of the controversy and to emphasize the importance of placing on record all future observations of land birds on the open Gulf, with notes describing the surrounding weather conditions. For a fuller understanding of the case for and against trans-Gulf migration, reference may be made to the following: Williams (1945, 1947, 1950, 1951); Lowery (1945, 1946, 1951); Bullis and Lincoln (1952).

Table 1 is an attempt to bring together all records of the species of land birds that have been identified over the waters of the Gulf at distances a mile or more from the nearest coast. It is to be hoped that this summary will stimulate additional observations of the same sort by providing a background against which they may be evaluated. The data were drawn from the following published or unpublished sources: Frazar (1881); Helmuth (1920); the anonymous account (1927) of observations on the S. S. *West Quechee*, designated as "*W. Q.*" in the table; Griscom (1945); Williams (1945); Lowery (1946), including, among other records, the observations by J. C. Howell and by personnel of the U. S. C. G. Cutter *Blanco;* Dufresne (1947); Packard (1947 and in litt.); Lowery's unpublished notes for 1948 and 1949; Paynter (1951 and in litt.); observations made by H. R. Bullis in 1950 and 1951, the latter incorporated in a paper by Bullis and Lincoln (1952). The number of individuals when stated is that recorded by the original observer, except in the case of Frazar, where "the most abundant," "very abundant," "abundant," "large numbers," and "quite a number" are all referred to in the table as "many." In order to condense the material for tabular presentation scientific names of species have been omitted except for the one species that does not appear in the A. O. U. Check List (1931) and has no standardized English name.

TABLE 1.—*Records of Land Birds Over the Open Gulf*

Species	Number	Distance offshore	Date	Source
Broad-winged Hawk	1	60 miles off Louisiana	Apr. 6	Bullis.
Buteos (spp.?)	1+	"10 miles or more"	[Spring]	Packard.
Duck Hawk	1	do	do	Do.
	1	16 miles off Louisiana	May 11	Lowery.
Pigeon Hawk	1	30 miles off Louisiana	Apr. 2	Frazar.
Sparrow Hawk	1	"Fairly close to land"	[Spring]	Williams.
Purple Gallinule	15	121–179 miles off Louisiana	May 4	Howell.
Florida Gallinule	1	60 miles off Louisiana	Apr. 6	Bullis.
Mourning Dove	A few	30 miles off Louisiana	Apr. 2	Frazar.
	1	177 miles off Yucatán	May 1	Lowery.
	1	204 miles off Yucatán	May 2	Do.
	1	25 miles off Louisiana	Nov. 17	Do.
Yellow-billed Cuckoo	8	121–179 miles off Louisiana	May 4	Howell.
Nighthawk (?)	50	18 miles off Yucatán	Sept. 3	Paynter.
Eastern (?) Nighthawk	3	121–179 miles off Louisiana	May 4	Howell.
	1	60 miles off Louisiana	Apr. 6	Bullis.
Ruby-throated Hummingbird	1	(?)	August	Griscom.
	2	40 miles south-southeast Pensacola	May 4	Bullis.
Belted Kingfisher	1	220 miles off Yucatán	Aug. 18	*Blanco.*
	1	100± miles off Louisiana	Mar. 29	Helmuth.
Erator inquisitor	1	Few miles off Southern Veracruz	Nov. 28	Paynter.
Eastern Kingbird	1	8–9 miles off Louisiana	Apr. 30	Lowery.
Oray Kingbird	1	32 miles off Louisiana	May 11	Do.
Eastern Phoebe	1	30 miles off Louisiana	Apr. 2	Frazar.
Empidonax sp.?	1	121–179 miles off Louisiana	May 4	Howell.
Olive-sided Flycatcher	1	60 miles off Louisiana	Apr. 6	Bullis.
Vermilion Flycatcher	1	do	do	Do.
Flycatchers (spp.?)	Many	30 miles off Louisiana	Apr. 2	Frazar.
Tree Swallow	Several	100± miles off Louisiana	Mar. 29	Helmuth.
	1	60 miles off Louisiana	Apr. 6	Bullis.
	(?)	"10 miles or more"	[Spring]	Packard.
Bank Swallow	1	224 miles off Yucatán	May 10	Lowery.

TABLE 1.—*Records of Land Birds Over the Open Gulf*—Continued

Species	Number	Distance offshore	Date	Source
	1	169–271 miles off Yucatán	May 5	Howell.
Barn Swallow	2	4–5 miles off Louisiana	Apr. 30	Lowery.
	1	21 miles off Louisiana	do	Do.
	1	61 miles off Louisiana	do	Do.
	1	67 miles off Louisiana	do	Do.
	1	82 miles off Louisiana	do	Do.
	2	101 miles off Louisiana	do	Do.
	4	119 miles off Louisiana	do	Do.
	16	149 miles off Louisiana	do	Do.
	3	248 miles off Louisiana	May 1	Do.
	3	190 miles off Yucatán	do	Do.
	7	154 miles off Yucatán	do	Do.
	12	121–179 miles off Louisiana	May 12	Howell.
	1	242 miles off Louisiana	Aug. 16	*Blanco.*
	1	228 miles off Yucatán	Aug. 26	Do.
	100+	"10 miles or more"	[Spring]	Packard.
	++	20–30 miles off Texas	do	Williams.
Cliff Swallow	1	(?)	August	Griscom.
	1	30 miles off Louisiana	Apr. 2	Frazar.
Purple Martin	100+	125 miles off Louisiana	Aug. 25	"H. Q."
	2	60 miles off Louisiana	Apr. 6	Bullis.
Catbird	2	121–179 miles off Louisiana	May 4	Howell.
	?	"10 miles or more"	[Spring]	Packard.
Robin	3	90 miles off Louisiana	Mar. 29	Helmuth.
Wood Thrush	20	30 miles off Louisiana	Apr. 2	Frazar.
Veery	2	121–179 miles off Louisiana	May 4	Howell.
Thrush (sp.?)	?	"10 miles or more"	[Spring]	Packard.
Eastern Bluebird	1	do	do	Do.
Red-eyed Vireo	1	do	do	Do.
Black and White Warbler	Many	30 miles off Louisiana	Apr. 2	Frazar.
	1	85–95 miles off Tampa	Mar. 31	Helmuth.
	3	60 miles off Louisiana	Apr. 6	Bullis.
Prothonotary Warbler	Many	30 miles off Louisiana	Apr. 2	Frazar.
	1	85–95 miles off Tampa	Mar. 31	Helmuth.
	1	60 miles off Louisiana	Apr. 6	Bullis.
Worm-eating Warbler	Many	30 miles off Louisiana	Apr. 2	Frazar.
	2	60 miles off Louisiana	Apr. 6	Bullis.
	1	[12 miles off Mississippi]	[Spring]	Packard.
Nashville Warbler	1	60 miles off Louisiana	Apr. 6	Bullis.
Parula Warbler	1	100 ± miles off Louisiana	Mar. 15	Lowery.
	1	83 miles off Yucatán	Mar. 14	Do.
	1	18 miles off Yucatán	Aug. 30	Paynter.
	(?)	"10 miles or more"	[Spring]	Packard.
	1	90 miles off Louisiana	Mar. 29	Helmuth.
	1	85–95 miles off Tampa	Mar. 31	Do.
Yellow Warbler	Many	30 miles off Louisiana	Apr. 2	Frazar.
	5	121–179 miles off Louisiana	May 4	Howell.
	1	196 miles off Louisiana	Aug. 25	*Blanco.*
	(?)	"10 miles or more"	[Spring]	Packard.
	1	60 miles off Louisiana	Apr. 6	Bullis.
	2	1 mile off Southwest Pass, La	Apr. 30	Lowery.
Magnolia Warbler	1	121–179 miles off Louisiana	May 4	Howell.
	1	60 miles off Louisiana	Apr. 6	Bullis.
Cape May Warbler	1	176 miles off Yucatán	May 10	Lowery.
	1	38 miles off Louisiana	Apr. 21	Do.
	1	226 miles off Louisiana	Apr. 22	Do.
Black-throated Blue Warbler	1	90 miles off Louisiana	Mar. 29	Helmuth.
Myrtle Warbler	A few	60 miles off Louisiana	Apr. 2	Frazar.
	1	90 miles off Louisiana	Mar. 29	Helmuth.
	Several	85–95, miles off Tampa	Mar. 31	Do.
	1	119–255 miles off Yucatán	Mar. 14	Lowery.
	1	45 miles south-southeast Pensacola	May 5	Bullis.
Black-throated Green Warbler	1	66 miles off Louisiana	May 11	Do.
Yellow-throated Warbler	2	60 miles off Louisiana	Apr. 6	Do.
Chestnut-sided Warbler	Many	30 miles off Louisiana	Apr. 2	Frazar.
	(?)	"10 miles or more"	[Spring]	Packard.
Bay-breasted Warbler	1	121–179 miles off Louisiana	May 4	Howell.
Black-poll Warbler	1	60 miles off Louisiana	Apr. 6	Bullis.
	1	119 miles off Louisiana	Apr. 30	Lowery.
Ovenbird	A few	30 miles off Louisiana	Apr. 2	Frazar.
Northern Water-thrush	(?)	"10 miles or more"	(?)	Packard.
Louisiana Water-thrush	1	121–179 miles off Louisiana	May 4	Howell.
Kentucky Warbler	9	60 miles off Louisiana	Apr. 6	Bullis.
	Many	30 miles off Louisiana	Apr. 2	Frazar.
	1	121–179 miles off Louisiana	May 4	Howell.
Mourning Warbler	Many	30 miles off Louisiana	Apr. 2	Frazar.
Common Yellow-throat	Many	do	do	Do.
	1	121 miles off Louisiana	May 11	Lowery.
	6	60 miles off Louisiana	Apr. 6	Bullis.
Hooded Warbler	Many	30 miles off Louisiana	Apr. 2	Frazar.
	1	(?)	August	Griscom.
	1	60 miles off Louisiana	Apr. 6	Bullis.
Canada Warbler	1	18 miles off Yucatán	Aug. 30	Paynter.
Wilson Warbler	(?)	"10 miles or more"	[Spring]	Packard.
American Redstart	Many	30 miles off Louisiana	Apr. 2	Frazar.
	1	90 miles off Louisiana	Mar. 29	Helmuth.
	1	16 miles off Louisiana	May 11	Lowery.
	2	121–179 miles off Louisiana	May 4	Howell.
	1	220 miles off Yucatán	Aug. 19	*Blanco.*
	1	60 miles off Louisiana	Apr. 6	Bullis.
Bobolink	1	210 miles off Yucatán	May 10	Lowery.
	1	30 miles off Louisiana	May 4	Dufresne.

TABLE 1.—*Records of Land Birds Over the Open Gulf*—Continued

Species	Number	Distance offshore	Date	Source
Orchard Oriole	1	94 miles off Louisiana	Apr. 30	Lowery.
	3	121–179 miles off Louisiana	May 4	Howell.
	1	60 miles off Louisiana	Apr. 6	Bullis.
Baltimore Oriole	1	121–179 miles off Louisiana	May 4	Howell.
Baltimore Oriole (?)	1	43 miles off Louisiana	May 11	Lowery.
Scarlet Tanager	Many	30 miles off Louisiana	Apr. 2	Frazar.
	1	60 miles off Louisiana	Apr. 6	Bullis.
Summer Tanager	A few	30 miles off Louisiana	Apr. 2	Frazar.
	1	60 miles off Louisiana	Apr. 6	Bullis.
Tanager (sp. ?)	1	121–179 miles off Louisiana	May 4	Howell.
Indigo Bunting	Many	30 miles off Louisiana	Apr. 2	Frazar.
	1	121–179 miles off Louisiana	May 4	Howell.
Painted Bunting	Many	30 miles off Louisiana	Apr. 2	Frazar.
Dickcissel	1	94 miles off Louisiana	Apr. 30	Lowery.
Red-eyed Towhee	A few	30 miles off Louisiana	Apr. 2	Frazar.
Henslow Sparrow	1	*ca.* 180 miles off Alabama	Mar. 30	Helmuth.

The table includes records of 64 species, 28 of which have been observed more than once. If the summary were to include the herons and sandpipers seen over the Gulf and discussed in the section on coastal birds, the total of nonpelagic birds definitely recorded at sea would be increased to 73 species. The seasons covered by these observations extend from March 29 to May 11 and from August 16 to November 28. Sixty-one of the species listed in the table have been observed in spring, but only twelve have been definitely seen in fall.

There are 140 entries in the table, and for 123 the approximate position of the observations is known. Among these 123 entries, only 3 represent birds seen less than 10 miles from land; only 9, less than 20 miles from land; and no more than 12, less than 30 miles from land. Thus the published data so far offer little to support the idea advanced by Williams (1945, 1947) that migrating birds cut chords of varying length across indentures of the coast, an idea, incidentally, at variance with experience of European observers who have studied the relation of migration routes to coast lines. While the waters rather close inshore are those most frequented by boats and therefore the waters over which maximal proportions of the birds present might be expected to be seen, it is highly questionable that the present records reflect the true relative abundance of land birds over various sections of the Gulf. Certainly many more land birds must have been seen from time to time over inshore waters than have been reported.

Moreover, the majority of the records are supplied by four observers: Frazar, Bullis, Helmuth, and Howell, who were, respectively, 30, 60, 80 (estimated), and 121–179 miles offshore from Louisiana when birds appeared in numbers on or near their boats. Just as concentrations of species and individuals in spring on land on the northern Gulf coast are associated with inclement weather, so are these exceptionally high counts at sea. Three of the notable concentrations occurred after the passage of moderate or severe cold-front storms and the coincident shift of the winds to the north, which imposed an obstacle to northward flight. But the fourth spectacular flight, that observed by Bullis, which involved thousands of small land birds, was recorded mainly when the winds were southerly, even though the skies were heavily overcast. In all cases where the direction of flight of land birds over the Gulf has been recorded, they were proceeding in the seasonal direction of migration. This has been the case irrespective of the direction of the wind at the time the observations were made.

The foregoing discussions should make it apparent that, in the present state of our knowledge, any record of any pelagic bird, or of any land bird, anywhere over the Gulf of Mexico, as well as of any coastal species seen offshore, has potential significance and is worth recording.

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CHAPTER XIX
MAMMALS OF THE GULF OF MEXICO

MAMMALS OF THE GULF OF MEXICO

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The mammalian fauna of the Gulf of Mexico consists of the manatee, the West Indian seal, and various cetaceans. In this account repetitions of keys and anatomical descriptions are omitted. An attempt has been made to include only information relating particularly to the Gulf.

Order PINNIPEDIA

Family PHOCIDAE. Hair Seals

Monachus tropicalis (Gray). West Indian Seal

The monk seals are restricted to warm waters of the Northern Hemisphere, and there are only three species. These are *Monachus monachus* (Hermann), of the Mediterranean and Black Seas, *M. schauinslandi* Matschie, of the Hawaiian Islands, and *M. tropicalis*, of the Gulf and West Indian region.

So far as scanty historical information goes the former range of the West Indian seal was from the Bahamas and southern Florida through the West Indies to Honduras and Yucatán. Gunter (1947) has given information indicating that single individuals and small herds occasionally visited the western Gulf as far north as Galveston, Texas, as late as 1932.

Large adults measure up to 7.5 feet in length. The color is "brown, tinged with gray, caused by the hairs being light at the extreme tip. The color becomes lighter on the sides, and gradually passes into pale yellow or yellowish-white on the ventral surface of the body." (J. A. Allen, 1887.)

Little is known of the natural history of the West Indian seal. J. A. Allen (op. cit.) and True and Lucas (1884) summarized practically all of the information. Several females with fetuses nearing full term were killed in December 1886 on the Triangle Keys off Yucatán. Food habits are unknown. Monod (1923) observed *M. monachus*, the Mediterranean species, chasing fish.

This animal was also called "sea-wolf" for no good reason, for it is mild and unsuspicious when on the beach. Glover Allen (1942) pointed out that the many Seal and Lobos Keys are reminiscent of its former presence. This unfortunate species was easily procurable and was the best source of oil in the southern islands during colonial times. This led to its early and rapid decimation. The famous English geographer and freebooter, Sir William Dampier, noted the fact in 1675. He found the seals in abundance in the Alacranes Islands and said, "the Spaniards do often come hither to make Oyl of their Fat." They were already becoming scarce when P. H. Gosse wrote about them in Jamaica in 1846. The story of their decline to near extinction is succinctly recorded by Glover Allen (op. cit.). The last specimen taken was killed at Key West, Florida, in 1922 (Townsend 1923). The last sight record was on the Texas coast in 1932 (Gunter, op. cit.).

However, it seems probable that a few still survive on the Triangle Keys and the Alacran Islands off the coast of Yucatán. Dr. Raymond M. Gilmore told the writer that residents of Carmen, Yucatán, reported seeing seals in the Alacrans as late as 1948. They were reported to come ashore in greatest numbers in April. Others may exist (Moore 1953). They should be rigidly protected.

Order SIRENIA. Sea Cows

Family TRICHECHIDAE. Manatees

Trichecus manatus Linnaeus. West Indian Manatee

Harlan (1824) described the Florida manatee as different from the West Indian or South American manatee and gave it the species name *latirostris*. True (1884) agreed that there were two species, but neither of these workers showed where the difference lies. True considered that the so-called Florida manatee also lived in the West Indies, while the South American manatee lived from along the mainland to far up into Mexico. This opinion also implies that the habitats are different

and that the two groups do not mingle. In view of the well-known wandering habits of manatees, especially in summer, this assumption seems quite improbable. Allen (1942) reviewed the case and said Hatt (1934) considered the two as racially distinct. Moore (1951) has shown that certain skull characters (indices of the foramen magnum) of a small series of specimens from Texas, Louisiana, and Florida did not show differences. The Texas specimens would presumably belong to the West Indian race, according to the summary of distribution given by Allen (op. cit.). Whether or not the small anatomical differences would stand up if a larger series were studied remains to be seen. In the meantime, it seems preferable to refer to the Floridian, West Indian, and northern South American manatees as one group.

The present and recent past distribution of *T. manatus* is from south central and southern Florida, through the West Indies and Antilles to Mexico, and southward throughout Middle America to British Guiana. There they seem to stop and do not overlap the range of *T. inunguis*, an inland species of the Amazon and adjacent regions. Northward, manatees extend up the coast of Mexico to Veracruz. This may be said to be the winter range for some manatees are wanderers in summer. They have been reported in the literature from the Carolinas and Virginia. Popular writings on natural history and newspaper accounts indicate, without much doubt, that they occasionally reach the coast of New Jersey. True (1884) mentioned the probable case of a manatee which was washed ashore dead on the Shetland Islands in 1785 and said it must have "set sail" from the Florida coast.

True quotes Silas Stearns on reports that manatees were formerly occasionally seen on the northern Gulf coast from Pensacola to New Orleans, and that their bones were formerly common. Gunter (1941) reported a skull from Louisiana and several specimens from Texas. True (op. cit.) said a South American manatee was taken in Texas in 1855. Formerly manatees visited the mouth of the Rio Grande every summer, coming from farther south in Mexico. At least three were captured alive there in 1911 and 1912 and were later exhibited over the country. They have been unreported for the past 10 years, probably because of population decline. In former times it is probable that manatees visited all coasts of the Gulf of Mexico in summer, although less abundantly to the north.

Manatees are extremely sensitive to cold, as has been reported many times, and are sometimes killed by cool weather as far south as the Florida Keys. It is most improbable that they lived the year-round on the northern Gulf coast, and they are continuous residents in the United States only in Florida. In the days when manatee populations were much more extensive, possibly they did leave bones in numbers along the northern Gulf coast, as stated by Stearns, and these may have been the result of early cold waves or winter kills. Moore (1953) has shown that manatees live quite far inland along some of the rivers of northern Florida and do not go south during the winter. Instead they move to the vicinity of large springs during cold spells where the water temperature never falls below 70° F.

Manatees, along with other sirenians, have the heaviest bone structure known, and the long bones are like ivory. They have paddle-like forelimbs and no hind limbs. They are pure vegetarians and inhabit coastal waters where their food grows. They are found occasionally in the open sea, near the shore. The upper lip is more or less cleft and the two halves can be manipulated independently. The Sirenia have no close relatives but seem to have distant affinity with the elephants. There are similarities of the skull, and these two groups alone among mammals have teeth which grow forward along the jaw to replace those which are worn away. Manatees are lethargic animals and can remain under water 12 minutes. Little is known about them and they should be carefully studied in their native haunts. According to Moore (1953) young Florida manatees have been reported for every month except December.

The late Capt. C. M. Scammon was noted as a chronicler of marine mammals wherever he went. In describing the general habits and appearance of manatees we can do no better than to quote his words (in part) from an unpublished manuscript: [1]

> The Sea-Cows may be regarded as among the most interesting creatures in their habits and disposition of all the marine mammals. Yet in respect to their form and general appearance, they seem like animals of a low order.

[1] Unpublished manuscript loaned by Joel W. Hedgpeth.

The general proportions of the Sea-Cow are like those of the Sea-Elephant and Seal. Its anterior limbs, or swimming paws, are short, thick, and rounded at their extremities. Its posterior limb, or tail—forms a thick oval lobe, slightly notched in the center of its termination.

Its head is tapering with a small rounded muzzle. Its comparatively small mouth is almost hidden from view, when the creature lies in a state of quietude.

Its very small dark eyes are devoid of expression. The general color of the Sea Cow is a dull black, but frequently white or clay colored patches or spots occur about the throat, neck and caudal extremities.

The approximate proportions of the animal is about 7 feet in length, and 6 feet in its greatest girth of body.

Our only opportunity for observing upon the habits of the Sea Cow was at Key West, Florida—1880—when two captured animals were enclosed in a broad shallow tank which, however, afforded the animals room to move about and around each other.

The actions of the strange creatures—as they appeared to us—were extremely interesting. Both of them seemed inclined to remain in a state of quietude, for whenever an attempt was made to move them about or roll them over, they would raise a plaintive cry, the sound of which, in its half nasal strain, was much like that of an infant. But the moment they were left undisturbed, they would lay quite motionless. Or if a movement was made, it was in a sluggish manner.

The geographical distribution of the Atlantic Sea-Cow is, or has been, about bays and large rivers and lagoons, which are near, or within the tropical limits of North and South America, and which are closely connected with ocean waters. Or from the northern coast of Florida to, and including the shores and savanas of the Amazon River. The last mentioned affording these herbivorous marine animals a vast and luxuriant feeding ground, where they roamed at will, and basked on shore, under a tropical sun, when not molested by their human pursuers. About the West India Islands, Sea Cows were in former years found in large numbers.

According to the accounts of old voyages, this marine vegetable eater abounded on the coast of Africa, in the same zone as those found upon the American coasts.

Although the natural food of the sea cow is the spontaneous herbage bordering low shores, or spreading over marshy regions, its fondness for more luscious subsistence is of peculiar interest.

The fact was verified by the two individuals brought to Key West. For when they were in a hungry state, the tender leaves of beets, as well as those of cabbage, would be eagerly devoured. Yet, when not craving food, they manifested much enjoyment in eating bananas, if peeled for them—and at such times, they would utter a sort of nasal or guttural strain of satisfaction, quite amusing. But the moment common grass, or the tops of turnips, were offered to them, they would utter their whining petulant cry of dissatisfaction as if they were weanlings.

Many writers testify to the Sea Cows' strong affection for their young offspring. And when attacked, the mother will sacrifice her own life, in her efforts to protect her charge. And during the time of a murderous onslaught, the lamentations of the parent animal are mentioned as deeply affecting to witness. Hence the name frequently mentioned by both sailors and hunters, *Lamentin*. Yet like their congeners, the Seal, Sea Otters, and Sea Elephants, the sea cows are rapidly approaching extinction and at the present time are only found in remote retreats.

Order CETACEA

Whales, Porpoises, and Dolphins

GENERAL INFORMATION

The adaptations superimposed upon the basic mammalian physiology of cetaceans to fit them for life in the sea has caused certain changes in respiration and circulation. Some of the larger whales sound to great depths and can stay submerged for more than an hour. They must withstand great pressures, rapid pressure changes, and long cessation of breathing. It seems clear that modifications of the pattern of mammalian physiology of breathing have taken place without development of new or greatly different processes. A concise review of certain facts of cetacean physiology has been given by Jeffrey (1951).

The Cetacea have no external hind limbs. The forelimbs are more or less flipper-like and serve as pectoral fins. Some whales have a dorsal fin, and some do not. Propulsion is by a tail which is stroked up and down. The lobes or flukes are horizontal.

Breathing is done through openings in the top of the head. In the toothed whales there is a single opening; the baleen whales have two openings. The lungs are exceptionally capacious.

Some adult whales possess a few scattered hairs over the head and lips, but many do not. As far as is known, however, they all have hair at some fetal stage. Teeth are more or less uniformly pegshaped. They may be present in both jaws or only in the lower jaw in the toothed whales. In the baleen whales teeth are present only in the unborn. Baleen is a series of horny plates with frayed edges which grows down from the roof of the mouth. It is manipulated in conjunction with the huge tongue of these whales in straining out the food.

The external opening of the ear is minute, and the canal is strongly occluded with wax. Nevertheless, a mounting body of recent evidence shows that cetaceans have a finely developed auditory sense and communicate by a series of whistles, grunts, and underwater bellowings. Over the

hydraphone a school of traveling porpoises sounds something like a pack of hounds yelping with their mouths closed. The bottle-nose dolphin whistles under water with simultaneous release of air. The noise-making of cetaceans is peculiar in that they have no larynx or voice box, and the sounds emanate from controlled movements of gas within the various air passages. Sinclair (1950) has recently shown that the auditory area of the brain of the bottlenose dolphin is exceptionally well-developed and that the olfactory nerve is minute. Toothed whales probably cannot smell. In contrast, the olfactory lobe of baleen whales is rather well-developed. The eyes are relatively small, and power of vision is weak in most species.

All cetaceans are covered with a layer of fatty areolar tissue, known as blubber, which lies just under the skin. Whale oil cooked out from this material was the primary objective of the whaler. In addition to being a great store of energy and an insulation wall, the blubber possibly serves as a reservoir for storage of oxygen during deep dives. This layer varies in thickness from an inch in smaller porpoises to 18 inches in large whales.

Young cetaceans are almost half the length of the mother when born although only one-tenth or less of her weight. They grow rapidly and are nursed for more than a year. The writer once measured a female bottlenose dolphin 8 feet 4 inches long, and her nursing calf 5 feet 7 inches long. Breasts are present on each side of the vaginal openings, extending forward, and can be seen as swellings of the abdominal outline. The nipples are retracted in two slits. The milk collects in large sinuses and is actively expelled at the time of nursing which takes only a few seconds. Whales mature at the age of 3 to 4 years. The age attained is unknown.

The toothed whales pursue individual prey and are known to live largely on fishes, squid, and cuttlefish. Some dolphins also eat shrimp, and certain fresh-water species possibly utilize some plant material. The killer whale varies the fish diet by attacking any other mammal found swimming in the water. The baleen whales feed by cruising with their large mouths agape, taking in planktonic crustacea, especially the euphausiids and copepods, and the pteropods. Occasionally, schools of small fishes are also engulfed. One baleen whale was found to have 2 tons of plankton in its stomach.

Some whales undertake long seasonal migrations extending over vast stretches of the oceans. They nevertheless may be rather sharply aggregated in definite localities at the different seasons, probably because of availability of food more than any other factor. These areas were called "grounds" by the old-time whalers and were given individual names.

Whales are comparatively intelligent animals. The brain is large, and the cerebral hemispheres are extensively convoluted. Studies of the play behavior and other activities of the bottlenose dolphin by McBride and his associates at the Marineland Aquarium in Florida have led them to rank the intelligence of this cetacean as lying somewhere between that of the dog and the chimpanzee (McBride and Kritzler 1951).

CETACEANS OF THE GULF OF MEXICO

The cetaceans of the Gulf of Mexico are not at all well-known, as far as actual records go, and it is only in recent years that some of the common porpoises and dolphins have been recorded. It may be assumed that practically all species known to the western subtropical Atlantic are found in Gulf waters.

Most actual records are known from infrequent strandings which have largely gone unnoted in the literature. The whalers of a century ago combed the seas of the world rather thoroughly, but they found no reason to sail often into the Gulf of Mexico or the Caribbean Sea. The closest whaling ground of any consequence was the "Charleston Ground" off the South Atlantic coast of the United States (Townsend 1935). This fact and the relative infrequency of strandings indicate that the cetacean population of the Gulf of Mexico, especially of larger species, is small in numbers.

In the following account only those species known from actual records are treated individually. Other species likely to be present are listed together.

Suborder ODONTOCETI. Toothed Whales

Family PHYSETERIDAE. Sperm Whales

Physeter catodon Linnaeus. Sperm Whale

This is the largest of the toothed whales and the largest predatory animal that ever lived on

earth. It is the one mammal swimming the seas for which the killer whales show some respect. The largest known males attain a length of 65 feet. Females are only about half this size or less. The sperm whale lives largely on giant squid which it seeks out at great depths. One was found entwined in a broken trans-Pacific cable which had to be raised from a depth of a thousand fathoms. It also feeds on octopuses and fishes.

There is no dorsal fin. The head is huge and rectangular, but the jaw is long and narrow. Teeth are present only in the lower jaw. The color is almost black above shading to lighter below. It is social in habit and was reported to congregate in schools of hundreds during days of former abundance.

This whale was the prime prey of the old-time whalers because it is a relatively slow swimmer, does not often sink when killed, and has large amounts of oil, a great part of which is stored in the head. Spermaceti, used in making fine candles, is also found in quantity in this whale. It is also the producer of the somewhat fabulously valuable ambergris, a substance now largely replaced by synthetic chemicals. Pursuit of this whale was started in the eighteenth century and was at its height during the middle of the nineteenth. Townsend (1935) plotted the locality of capture of 53,877 whales by 744 vessels on 1,665 voyages out of New England ports from 1761 to 1920. He had logs of something less than 10 percent of the American vessels operating during this time. His data show that between 60 and 100 sperm whales were taken in the Gulf during this period. The total from all ships must have been closer to a thousand. None were taken in the western Gulf, and the westernmost was a little beyond the mouth of the Mississippi. All captures were made in the months of March to July. A slightly greater number were taken in the Caribbean Sea. All Caribbean catches were made in March, April, and May, as the whales returned from the south. Townsend's maps indicate strikingly, as the whalers well knew, that the sperm whale goes south of the Equator in winter and returns to northern temperate waters in summer, staying mostly between the parallels of 50° N. and S.

One stranding of a sperm whale on the east Texas coast was reported by Newman (1910). Moore (1953) has recorded two strandings on the west Florida coast in 1939. One was a fetal male.

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Family KOGIIDAE. Pygmy Sperm Whales

Kogia breviceps (Blainville). Pygmy Sperm Whale

The pygmy sperm is an uncommonly reported cosmopolitan animal which possibly is often confused with larger porpoises and thus thought to be rarer than it actually is. The maximum length is around 13 feet. It is more or less black and has a dorsal fin. Like its larger relative, it has teeth only in the lower jaw and produces spermaceti. As far as is known, it lives largely on cuttlefish. Enders (1942) has given a description and listed much of the literature on strandings.

Moore (1953) reported the stranding of a female 9½ feet long on the beach of Pinellas County, Florida, in November 1949. It gave birth to a calf 5 feet 4 inches long, weighing 181 pounds. This is the only known record from the Gulf of Mexico.

Family ZIPHIDAE. Beaked Whales

The beaked whales are related to sperm whales and produce spermaceti. They have prolonged snouts similar to the dolphins and have only two teeth, both in the lower jaw. They have a dorsal fin. The midpoint of the flukes projects, and there are two grooves along the throat.

Ziphius cavirostris Cuvier. Goose-beaked Whale

This is a cosmopolitan animal which attains a length of 20 feet. The color may be black to gray above and sometimes white on the head and back. The two teeth are in the tip of the lower jaw. Moore (1953) has listed strandings in Pasco and Manatee Counties on the Florida Gulf coast and one on the west side of the Keys.

Other Beaked Whales

True's beaked whale, *Mesoplodon mirum* True, is known from the southeastern United States coast and probably enters the Gulf. It reaches a length of 16 feet and is dull black above. The teeth are on the outer tip of the jaw. The Gulfstream beaked whale, *Mesoplodon europaeus* (Gervais), has been reported from the ocean side of Key Largo in 1935 (Moore 1953). This is very close to the Gulf, and the species is to be expected there.

Family DELPHINIDAE. Porpoises and Dolphins

These are small to medium-sized toothed whales with numerous uniform teeth in both jaws. Some enter fresh water, and some species in South America, India, and China live there entirely.

The dolphins of the ancients were mammals. During the time of heraldry the word was confusedly applied to both the mammals and a fish. Today, the double usage still exists, and in popular usage the term is more often applied by laymen, at least in the United States, to the fish, *Coryphaena*. The true dolphin is a delphinid with a beak-like snout. The porpoises have a rounded snout, more or less flush with the mouth. The difference is not recognized by laymen, who usually refer to all members of this group as porpoises.

***Stenella plagiodon* (Cope). Long-snouted Dolphin**

The approximate size limit of this dolphin is 7 feet in length. It is found on the South Atlantic coast of the United States and most of the Gulf of Mexico. It was only recorded from the western Gulf a few years ago (Gunter 1941). Moore (1953) has given many records for Florida, some of which indicate that the animal leaves northern Florida waters in winter. Lowery (1943) records it from Louisiana. It is common in offshore waters and is quite often seen in schools of 50 or more. The habitat is oceanic, and it is seldom seen within 12 miles of the beach. The base color is purplish gray, and the back is thickly studded with white spots. Calves are uniformly gray. This dolphin often swims just ahead of ships and plays about them for long distances. It feeds on fish (Kellogg 1940). The southward extension of its range and most points concerning its natural history are unknown.

***Steno bredanensis* (Lesson), 1817. Rough-toothed Dolphin**

Miller (1924) reported one specimen from Tampa in 1902. The skeleton is in the U. S. National Museum. This dolphin is known from the warmer Atlantic and Indian Oceans. Moore (1953) questioned the record on the ground that the specimen might have been brought in aboard ship.

***Tursiops truncatus* (Montague). Bottlenose Dolphin**

This is the common "porpoise" of the Atlantic coast of the United States and the Gulf of Mexico. It also lives on the European coasts. The largest males reach a length of 12 feet. The color is almost uniformly purplish gray on the back shading to lighter beneath. A dorsal fin is present.

This dolphin inhabits shallow coastal waters and is often found in low salinity bays and very shallow water. Occasionally, it is seen 4 or 5 miles out to sea. More is known of its habits and life history than of any other cetacean. True (1891) observed the animals taken in a commercial fishery for them in North Carolina and recorded many facts. Wislocki and Enders (1941) were able to study placentation and fetal membranes more completely than has been done for any other cetacean. Gunter (1942) made some contributions to natural history, especially concerning food habits in Texas bays. There have been several observations of this animal in captivity beginning with Townsend (1914). McBride and his associates have made particular studies of behavior, intelligence, birth and postnatal care as exhibited by these dolphins at Marineland, Florida. The most recent paper is that of McBride and Kritzler (1951).

In the Texas bays they often venture out on to the flats near shore in pursuit of mullet, *Mugil cephalus* Linnaeus, which forms a very high percentage of their diet. In deeper waters they subsist mainly on the sand trout, *Cynoscion arenarius* Ginsburg, the spot, *Leiostomus xanthurus* Lacépède, and the croaker, *Micropogon undulatus* (Linnaeus). Nevertheless, they will feed upon almost any species of fish and have been reported to eat the hardhead catfish, *Galeichthys felis* Linnaeus, first chopping them in two just back of the dorsal spine. Sports fishermen complain because they chop tarpon and sailfish off of lines after they are hooked. They are also known to eat sting rays. They will even ingest very small specimens of needle gar (*Strongylura*) and puffers (*Sphoeroides*). They apparently feel an enmity toward sharks and sometimes engage in vicious battles with them. Their stomachs have been found containing large hunks of shark flesh. Although they have from 22 to 24 peg-shaped teeth in each jaw, dolphins prefer to swallow their prey whole, and if fishes are removed from their stomachs after being recently swallowed, they are found to have not a scale disturbed. One shrimp, *Penaeus setiferus* (Linnaeus), was found among some 500 fishes taken from dolphin stomachs in Texas. The late E. A. McIl-

henny has reported finding dolphins with a bucketful of freshly eaten shrimp in their stomachs. Kleinenberg (1938) reported finding one shrimp among thousands of fishes in the stomach of this dolphin in the Black Sea. The bottlenose dolphin causes considerable trouble to the shrimp fishermen because it tears holes in their trawls in efforts to get at the fish and shrimp within. They report that the animal can distinguish change in the engine beat when the trawl is lowered and will come from long distances to where a drag is being made.

Wislocki and Enders (1941) have shown that the embryos are carried in the left uterine cornu. Gunter (1942) has shown that the length of dolphins at birth is 44 inches and more. Several stillbirths and some successful ones have been observed by McBride and Kritzler. In all cases the young were born tail first. The mother does not bite the umbilical cord in two but whirls in a characteristic fashion and breaks it. The baby makes its way unaided to the surface at once and begins to breathe. In cases of stillbirth, however, the mother tries to lift the young, sometimes being aided by other females. Moore (1953) found a female in the wild holding her decayed young to the surface. He judged the baby had been dead at least 3 days. The babies post themselves a little above and behind the dorsal fin of the mother. Other females apparently try to help the mother in protecting the young and often the little dolphin swims between the mother and another female. From the time of birth they can swim fast enough to keep up with adults swimming at a fairly high rate of speed. When a baby is temporarily lost from its mother, it swims in a tight circle and whistles until she comes. The preceding information is taken from McBride and Kritzler (1951).

Dolphins can be overtaken with outboard motorboats at a speed of 22 miles per hour. The maximum speed of 60 miles per hour often popularly accredited to these animals is a preposterous overestimate.

Male porpoises fight viciously during breeding periods and acquire many scars from these battles. They are sometimes seen milling about in water tinged with their blood. Gunter (op. cit.) found that the size of the fetuses increased from December to April, and the first young were taken in April. On the other hand, McBride and Kritzler (op. cit.) think that there is no special breeding season. They say that the calves are nursed for 18 months and that the females in captivity do not reproduce more than once every 2 years.

The bottlenose dolphin seems to rank rather high in the intellectual scale of the mammals. In captivity the young have been observed to invent little games which are played alone or with the help of a human partner. Interested readers should consult McBride and Kritzler (op. cit.) and papers cited therein.

The numbers of these dolphins are not extensive enough for any commercial enterprise to be centered on them, although their flesh is good food. They have not been the cause for declines of fishes as is sometimes stated. They were present in much greater numbers years ago, when apparently all life in the shallow bays was also more abundant, and they seem to have declined in numbers during the past 50 years. Writers of years ago reported that the bays of the Gulf coast formerly teemed with these dolphins. Now they are numerous only in the passes leading from the bays to the Gulf.

Grampus orca Linnaeus. Atlantic Killer Whale

This species is widely distributed in the seas of the world. There is a different species in the North Pacific. As Kellogg (1940) said, they fear nothing that lives. They usually travel in packs and ferociously attack all other marine mammals including the larger whales. They grow to a length of 22 feet or more and have capacious gullets which enable them to swallow seals and the smaller porpoises whole. Their diet is varied by larger fishes.

The high dorsal fin and conspicuous white spots back of the eye and under and behind the dorsal, and the white belly are identifying marks. The latter area extends up on the side posteriorly.

Moore (1953) has given several records from the Atlantic side of south Florida. There are no records from the Gulf, based on actual specimens, but they are to be expected, and one was sighted 35 miles southeast of Port Aransas, Texas, in the summer of 1951 by Capt. R. C. Van Zandt, who is well acquainted with the Pacific species and its depredations on the west coast of Mexico.

Globicephala macrorhyncha (Gray). Short-finned Blackfish or Pilot Whale

Blackfish are large, black oceanic porpoises which feed largely on squids and fishes. They travel in large schools. The globular head, especially of the males, is a distinguishing character. They attain a length of 20 feet. Lowery (1943) made photographs and measured several specimens of a school of 49 which were found stranded on the beach near Bayou Lafourche, Louisiana, following the hurricane of August 1940. Gunter (1946) recorded four specimens from the Texas coast and two probable records, all from strandings. Since then, three other strandings have come to attention, and another skull was obtained. These were all from Mustang and Padre Islands, one coming from Brazos Santiago at the southern tip of Texas. One small school was seen near the beach of Mustang Island in October 1949. Lowery recorded this porpoise under the name of *G. ventricosa* (Lacépède), the North Atlantic species, and the writer followed his conservatism. All specimens the writer has seen have the short fin described by Cope, and it has been concluded that his *brachyptera* is definitive for the Atlantic and Gulf species of the southern United States. It is, however, only a synonym of *Globicephala macrorhyncha* (Gray) as recently shown by Fraser (1950). This animal is found over the tropical Atlantic.

The blackfish is noted for following the leader into the beach and stranding, thus the name pilot whale, and for making bellowing, grunting noises at these times. Moore says strandings of this species exceed all others put together in Florida, and he has recorded instances of 46 and 200 animals stranding at one time.

Other DELPHINIDAE

The following species are not recorded from the Gulf of Mexico but may be expected:

The common dolphin, *Delphinus delphis* Linnaeus, is known from most tropic and temperate seas. It usually is found more than 10 miles offshore but has been known to invade rivers. The closest known record is Miami, Florida (Moore, op. cit.). The same writer lists *Stenella frontalis* (Cuvier) from Dade County and *S. longirostris* (Gray) from the Bahamas. These tropic and Southern Hemisphere dolphins may enter the Gulf. The false killer, *Pseudorca crassidens* (Owen), has been recorded from Broward County on the southeast Florida coast. The grampus, *Gamphidelphis griseus* Cuvier, may be expected because of its general distribution.

Suborder MYSTICETI. Baleen Whales

Family BALAENOPTERIDAE. Finbacks, Rorquals

Balaenoptera physalus (Linnaeus). Common Finback

Lowery (1943) listed three records of *Balaenoptera* sp. stranding on the Louisiana coast. There have been strandings of baleen whales on the Texas coast, but these animals have not been definitely identified or recorded, with one exception. On February 21, 1951, a small whale, 18 feet long, was found on the beach 22 miles east of Galveston. It was the common finback and was evidently very young and probably newborn. An account has been given by Breuer (1951). This is the only definite record from the Gulf of Mexico.

Balaenoptera acutorostrata Lacépède. Piked Whale

One specimen washed ashore on the Gulf beach of Wakulla County, Florida, in 1940. The remains of the skeleton were examined by Moore (op. cit.). There are several records from New England, but this whale is probably rare in southern seas.

Other Baleen Whales

The above two species are the only baleen whales definitely recorded from the Gulf of Mexico. The Sei whale, *Balaenoptera borealis* Lesson, and the humpback, *Megaptera novaeangliae* (Borowski), may be expected. Townsend's (1935) whaling records showed that the humpback was taken north of Haiti and in the Lesser Antilles and within 70 miles of the Florida Keys. The blue whale or sulphur bottom, *Sibbaldus musculus* (Linnaeus), may also be expected in the Gulf. This species is known to attain a length of 103 feet and is the largest animal that ever lived. Baughman (Jour. Mammal., vol. 46, pp. 392–393, 1946) gave a record of a baleen whale 70 feet long which stranded north of Freeport in 1940. From photographs he concluded it was *Sibbaldus musculus*, but there is no confirmation.

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CHAPTER XX
POLLUTION OF WATER

ASPECTS OF WATER POLLUTION IN THE COASTAL AREA OF THE GULF OF MEXICO [1]

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Principal natural resources of the Gulf that appear susceptible to damages from water pollution are sport and commercial fin fisheries, shellfisheries, wildlife, and recreational areas that are utilized by local people or attract tourists.

Through the Mississippi River alone, the Gulf receives drainage from 1,244,000 square miles, or 41 percent of the land area of the United States. Water comes from points as far distant as Bozeman, Montana, and Jamestown, New York, and from land fronting on the Gulf itself. Damaging pollution occurs locally at many upstream points of this and other long river systems. Because of natural purification and great distances of flow to the Gulf such pollution need not be considered here. With the exception of sediment loads, which may be carried great distances with little change in character, significant sources of pollution are those located near the Gulf.

The data upon which this report is based relate principally to sources of pollution lying within 50 miles of the Gulf. Pollution sources lying outside this zone are considered only if they are particularly significant by virtue of their specific quality or quantity. The land area so defined includes parts of Florida, Alabama, Mississippi, Louisiana, and Texas. Except with respect to shellfish sanitation, very few water pollution studies have been published. As a result, most information on this subject is found unpublished in the files of State health departments and water pollution control agencies. The most intensive investigations have been conducted by private organizations and were initiated by allegations of damages to oyster resources by petroleum industry wastes. Pending litigation and threatened litigation have kept reports of most of the findings from publication. A number of studies conducted by various agencies have been published (Gunter 1942; Anonymous 1949; Specht 1950; Phelps and Barry 1950; Anonymous 1952; Galtsoff et al., 1935; Galtsoff 1936).

The accuracy of data on water pollution is necessarily short-lived, principally because progress is continually being made as more municipalities and industries take action to abate pollution. This chapter is based on information available in 1953. Up-to-date information for specific areas may always be obtained from appropriate State agencies.

NATURE OF POLLUTION AFFECTING THE GULF WATERS

Wastes of various kinds enter the Gulf waters by direct discharge from coastal municipalities and industries or through tributary streams that serve as transmission media for wastes from considerable areas. Included are raw and partially treated municipal sewage, industrial wastes characteristic of a great variety of manufacturing processes, and sediment loads from soil erosion.

Municipal sewage is a complex mixture of the liquid-carried wastes that result from modern human existence. Although it is about 99.9 percent water, the solids making up the remaining 0.1 percent are the cause of the problems of sewage pollution. The discharge of untreated sewage to watercourses is objectionable mainly because of three of its characteristics: (1) actual or potential presence of pathogenic bacteria that threaten the health of persons using the water and cause economic losses to the shellfish industry by making the product unsafe for human consumption, (2) organic constituents that have a biochemical demand upon oxygen resources of the water so that aerobic organisms suffocate, and disagreeable odors and appearance from putrefaction become a nuisance, and (3) a solids content that makes the

[1] Assistance was given by State water pollution control agencies and shellfish sanitation agencies in the preparation of this report.

water unsightly and blankets the bottom and its population of organisms with layers of putrescible particles.

Industrial wastes vary in character with the nature of the industrial process in which they originate. Organic wastes, such as those from food processing, sugar refining, or pulp and paper making, are similar to sewage in their ability to diminish oxygen resources. In most cases, however, the oxygen demand per unit volume is greater than that of sewage and the pollution effects more drastic. Various chemical plants, metal industries, and oil field operations have wastes with high inorganic content. Discharges of such wastes cause damaging pollution if they make aquatic environments uninhabitable for desirable organisms, or if the receiving water becomes less suitable for any human usage. Once in the water, some wastes of this kind are dissipated appreciably only by dilution.

Sediment loads, which have their origin principally in soil losses from the land, enter the Gulf, its estuaries, lagoons, and contiguous lakes in some degree through every tributary stream. Data on sediment loads are available only for the principal contributors. The annual load of the Mississippi River alone is some five hundred million tons (Matthes 1951), and the load from all sources may bring the total to a billion tons or more. Aside from the losses of valuable soil resources, deposition of sediment loads along the coastal zone has raised serious problems in development and maintenance of navigation channels and harbor installations and has destroyed valuable shellfish growing areas.

WATER POLLUTION CONTROL AGENCIES, PROGRAMS, AND LAWS

Under provisions of the Water Pollution Control Act (Public Law No. 845, 80th Congress), the Division of Water Pollution Control of the Public Health Service participates, along with the States, in water pollution control activities; however, the primary rights and responsibilities in controlling water pollution rest with the States.

For the purposes set forth in the act, the country has been divided into major river drainage basins, and 9 field offices have been established to permit close, effective cooperation with State water pollution control agencies. Three such drainage basins have frontage on the Gulf of Mexico. A river basin office in Atlanta, Georgia, is concerned with water pollution activities in Florida, Alabama, and Mississippi. Another in Little Rock, Arkansas, has corresponding functions in Louisiana and Texas.

The ultimate aim of the cooperative activities is to abate and prevent water pollution in the United States. One step toward accomplishing this is the development of comprehensive programs for eliminating or reducing pollution. Basic in such development is recognition that a number of interests such as public health, wildlife and conservation, industry, municipalities, and agriculture have a stake in formulation of the program, its execution, and its cost. Each program will apply to an entire watercourse, or significant part as a unit, and will set down the pattern of remedial and preventive measures that will permit full utilization of the water resources for all present and potential water uses.

Evaluation of the present problem in each major drainage basin on the basis of presently available information has been completed. Reports on three of these areas contain data of significance with respect to the Gulf.[2]

The Water Pollution Control Act authorized the appropriation of funds for grants-in-aid to official State water-pollution control agencies to be expended by them in the conduct of investigations, research, surveys, and studies related to the prevention and control of water pollution caused by industrial wastes. Each of the Gulf States now has an active program along these lines. Encouragement of cooperative activities by the States and in the enactment of uniform State laws relating to water pollution, the collection and dissemination of information on the subject, provision of technical assistance with specific problems, and participation in the formulation of water-quality objectives are other phases of the overall program.

Pollution control activities of the individual Gulf States are related to and largely dictated by provisions, powers, and duties set forth in their existing legislation. Pertinent facts for each State follow.

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[2] Summary Reports on Water Pollution: (1) Western Gulf Drainage Basin, (2) Southwest-Lower Mississippi Drainage Basin, and (3) Southeast Drainage Basin 1951.

FLORIDA

Authorization to control water pollution is vested in the State Board of Health by legislative act (Ch. 381.43 and 387.08, Florida Statutes, 1941) and is implied by the enabling act authorizing the creation of a Sanitary Code by the State Board of Health (Ch. 381.50, Florida Statutes, 1941). Two other State agencies have limited authority in this field. The Commission of Game and Freshwater Fish has the power and authority to enforce the prohibition against the placing of certain deleterious substances or forces into fresh waters whereby fish are or may be injured. The State Board of Conservation is given authority to promulgate regulations to prevent action in one watershed area or location which will adversely affect the surface or underground water supply in another area.

ALABAMA

Responsibility for water pollution control activities in Alabama is vested largely in the Water Improvement Commission with comprehensive powers of enforcement, including the issuance of permits for the discharge of waste into the waters of the State. The State Department of Health has general authority with respect to enforcement of laws relating to public health and specific authority with respect to protection of drinking water. The State Department of Health also has responsibility for cooperating with the Water Improvement Commission in conducting investigations, inspections, and related activities.

MISSISSIPPI

Water pollution control is administered in Mississippi by two State agencies. The State Board of Health has authority to control water pollution through its general public health powers. The Game and Fish Commission has pollution control powers which specifically include the authority to hold hearings, issue regulations and final orders, and provide for judicial review of such orders, and is enabled to control pollution for the protection of game, fish, and wildlife.

LOUISIANA

Authority in Louisiana relating to water pollution control is vested in the Stream Control Commission, State Board of Health, and Louisiana Department of Wildlife and Fisheries. The Stream Control Commission has the general power and duty of administering all pollution control laws of the State that are broad and comprehensive. It may adopt standards, make investigations, hold hearings, and has enforcement powers. The State Board of Health has pollution control authority relating to public health. The Department of Wildlife and Fisheries enforces the Commission's orders, rules and regulations relative to pollution.

TEXAS

Water-pollution-control authority is vested in the State Board of Health and the Game and Fish Commission. The Office of the Attorney General acts as legal counsel to the enforcement agencies. The General Land Office, in cooperation with the Game and Fish Commission, establishes rules and regulations to prevent pollution on State-owned lands including tidelands. The State Board of Health has general pollution-abatement functions with specific emphasis on public-health aspects. The State Board of Health may set standards for drinking water, may review plans and specifications, make investigations, and hold hearings. Enforcement is by writ of injunction under civil statute and fines under penal code as issued by court. The Game and Fish Commission deals with matters protecting fish and oysters. A Water Pollution Advisory Council serves as a consultative and advisory body to other agencies, affected groups and industries.

FEDERAL-STATE SHELLFISH CONTROL PROGRAM

The sea-food products most affected by pollution of tidal waters, particularly from the public-health point of view, are the edible bivalve mollusks, oysters, clams, and mussels. During feeding these mollusks may retain from the overlying waters any pathogenic organisms which may be present along with their normal food materials. Since the commercially valuable edible mollusks are fixed by biological factors to those waters along the coast which are more or less diluted by fresh-water runoff from adjacent land bodies, it is obvious that some pollution of these shellfish-growing beds is unavoidable.

Adequate administrative controls over shellfish production must exist if outbreaks of typhoid fever and other enteric diseases carried by shell-

fish are to be avoided. This was pointedly brought out during the winter of 1924–25 when a series of typhoid outbreaks was traced to contaminated oysters which had been shipped from one packer to several large cities in the United States (Lumsden et al. 1925). Following this, basic control patterns were drawn up between the shellfish industry, the State health departments, and the United States Public Health Service. The Bureau of Chemistry of the United States Department of Agriculture (now the Food and Drug Administration of the Federal Security Agency) and the Bureau of Fisheries of the United States Department of Commerce (now the Fish and Wildlife Service of the United States Department of the Interior) were involved in this early planning.

Under this arrangement, the Public Health Service develops recommended standards and manuals of operating practice (Anonymous 1946) which are applied by the shellfish industry under the supervision of the State shellfish-control agencies. The Public Health Service evaluates these control procedures of the State agencies on a continuing basis. When satisfied that proper controls are exerted by the States, the Public Health Service publishes routine lists of shellfish shippers who are certified by the individual State shellfish-control authority, usually the State department of health. These lists are distributed widely throughout the United States to health officials and others who may be concerned with the problem of market quality of raw shellfish. In practice, a shellfish shipper finds it necessary to be properly certified in order to be able to market his products in most parts of the United States.

As in the case of most of the shellfish-producing States, the States bordering on the Gulf of Mexico divide the controls over shellfish operation between two State agencies. The purely sanitary aspects of the control program, including surveillance over the sanitary quality of shellfish-growing beds and operation of packing houses, rest with the individual State health department. Actual control of shellfish-growing areas which are closed to commercial fishing, on the other hand, is handled by some other State agency. In the case of Florida, the State Board of Conservation bears this responsibility, while in Alabama the State Conservation Department is involved. The Mississippi Seafood Commission patrols growing areas closed because of pollution in that State. In Louisiana, the Division of Oysters and Water Bottoms of the Department of Wildlife and Fisheries assists the State Department of Health in patrolling the closed areas. The Texas Game and Fish Commission cooperates with the Texas State Department of Health on patrol work in that State.

In the following pages areas closed to commercial harvesting of shellfish are described specifically on the basis of information resulting from sanitary and bacteriological surveys conducted by the several State departments of health. In most instances the results of such surveys are contained in reports cited in an annotated bibliography (Anonymous 1952).

SUMMARY OF WATER POLLUTION DATA

The summary set forth below is based entirely upon readily available information from various sources, and no investigations have been made specifically for the purpose of this report. The data therefore are admittedly incomplete. This is particularly true of industries and pollution caused by their wastes. Gaps in the data are nonetheless significant and point the direction of necessary future work.

Because of tremendous quantities of available dilution water, it is unlikely that pollutional wastes originating in the coastal area have appreciable effects upon either water or resources in the open waters of the Gulf. Reports of such effects have not been forthcoming, and no intensive investigations appear to have been made. On the basis of information now available, however, there are at least 369 separate sources of pollution that may have localized effects upon coastal waters of the Gulf or the lower reaches of tributary streams. One hundred ninety-seven of these are municipalities, sewer districts and institutions that utilize tributary watercourses, sloughs, lagoons, estuaries, and bays to dispose of their wastes. The sewer systems concerned serve a total of about 3 million persons. Industrial wastes of unknown character and quantity are also discharged to these sewer systems. Sewage from 35 municipalities with a total of 755,000 sewered inhabitants reaches surface waters without treatment of any kind. Numerical data on treatment loads or plant efficiencies are not

available for the 162 municipalities that provide treatment so that the actual total discharge for all municipalities is not known.

Because summary data on industrial wastes are not available for Texas and are less complete than municipal data for other Gulf States the extent of the industrial waste pollution problem is not fully shown. On the basis of present knowledge, 173 industrial plants of various kinds discharge treated or untreated waste directly to surface waters. These plants include production of pulp and paper, sugar, petroleum and its products, processed food, chemicals, and metals. Their wastes are of many different kinds. One hundred fifteen plants produce organic wastes, but the quantity can be estimated with confidence for only five, which discharge a total of 76,000 population equivalent.[3] Inorganic wastes are produced by 67 plants, and the type of wastes from five plants is not known. A number of plants have process wastes with appreciable quantities of both organic and inorganic components. Considerable additional information is needed before an estimate of the total quantity of waste from all sources can be made.

Although 82 percent of the municipalities along the Gulf coast that have sewer systems also have sewage treatment facilities, at least 25 percent of the total sewered population is not served by such facilities. In addition, recent phenomenal population growth and obsolescence of equipment have made 60 of the 162 existing sewage treatment facilities physically inadequate to satisfactorily treat the waste they receive.

Definite information on provision of pollution prevention measures or practices by industries is available for only about one-third of the plants. Less than one-third of these have treatment facilities of which two have insufficient capacity and three have unsatisfactory operation.

An increase of approximately 14 percent in the number of municipal treatment facilities will be necessary to help bring about an adequate pollution abatement program for the receiving waters. These new facilities, which are 22 in number, would serve about 130,000 people. In addition, 37 percent of the existing facilities need either to be replaced by new plants or enlarged and remodeled to handle existing loads in an adequate manner. These plants now serve about 272,000 persons.

Information on necessary remedial measures is available for only 14 percent of the industries. The facilities for 13 industries are known to be satisfactory, 9 new facilities are needed, and 3 need enlargements or additions.

Distribution by States of basic data on water pollution is shown in tables 1 through 4 and maps, figures 1 and 2. These are self-explanatory.

[3] Sewered population equivalent of industrial waste is based on 0.167 pounds of 5-day, 20° C. biochemical oxygen demand per capita per day in municipal sewage.

TABLE 1.—*Municipal sources of pollution in the coastal area of the Gulf of Mexico* [1]

1 State	2 Number of municipalities [2]	3 Total sewered population	4 Municipalities with sewage treatment	5 Population served	6 Municipalities without treatment	7 Sewered population
Florida	61	470,050	48	432,850	13	37,200
Alabama	12	161,500	10	159,400	2	2,100
Mississippi	8	65,500	7	55,500	1	10,000
Louisiana	30	821,300	22	205,850	8	615,450
Texas	86	1,491,450	75	1,401,200	11	90,250
Total	197	3,009,800	162	2,254,800	35	755,000

[1] Sources lying within 50 miles of the Gulf plus several significant sources lying just outside the 50 mile zone.
[2] Cities, towns, villages, sewer districts, and institutions.

TABLE 2.—*Industrial sources of pollution in the coastal area of the Gulf of Mexico* [1]

1 State	2 Number of plants	3 Treating wastes	4 Not treating wastes	5 Existing treatment facilities undetermined	6 Producing organic wastes	7 Producing inorganic wastes	8 Undetermined type of waste
Florida	47	9	1	37	31	17	1
Alabama	10	0	6	4	8	1	1
Mississippi	12	0	7	5	9	1	2
Louisiana	104	10	30	64	67	48	1
Texas							
Total	[2] 173	19	44	110	[3] 115	67	5

[1] Sources lying within 50 miles of the Gulf plus several significant sources lying just outside the 50-mile zone.

[2] Total adjusted for duplication shown in [3].

[3] Fourteen of these plants produce inorganic wastes also.

TABLE 3.—*Needs for abatement of water pollution in the coastal area of the Gulf of Mexico* [1]

1 State	2 Source	3 New plants	4 Sewered population	5 Replace existing plants	6 Sewered population	7 Additions or enlargements	8 Sewered population	9 None	10 Sewered population	11 Undetermined	12 Sewered population
Florida	Municipal	10	31,800	24	116,050	4	41,200	17	271,500	6	9,500
	Industrial									46	
Alabama	Municipal	2	2,100	3	3,700	2	4,300	5	151,400	0	
	Industrial	6								4	
Mississippi	Municipal	1	10,000	0	0	0	0	7	55,500	0	0
	Industrial									12	
Louisiana	Municipal	0		3	15,800	3	15,100	23	789,950	1	4,50
	Industrial	3				3		11		85	
Texas	Municipal	9	85,350	7	10,700	15	66,200	53	1,328,900	2	3,00
	Industrial										
Municipal total		22	129,250	36	145,250	24	126,800	104	2,592,450	11	16,0,50
Industrial total		9				3		13		147	
Total		31	129,250	36	145,250	27	126,800	117	2,592,450	158	16,0,50

[1] Sources lying within 50 miles of the Gulf plus several significant sources lying just outside the 50-mile zone.

TABLE 4.—*Existing industrial waste treatment facilities in the coastal area of the Gulf of Mexico* [1]

1 Type of industry	2 State	3 Number of plants	4 With treatment facilities	5 Without treatment facilities	6 Undetermined
Paper and allied products	Florida	3	1	1	1
	Alabama	5	0	5	0
	Mississippi	1	0	1	0
	Louisiana	2	1		1
	Texas				
Area total		11	2	7	2
Food and kindred products	Florida	23			23
	Alabama	3			3
	Mississippi	1			1
	Louisiana	49		24	25
	Texas				
Area total		76		24	52
Leather and leather products	Florida	3			3
	Alabama				
	Mississippi				
	Louisiana				
	Texas				
Area total		3			3
Chemical and allied products	Florida	17	8		9
	Alabama				
	Mississippi	8		5	3
	Louisiana	9	3	2	4
	Texas				
Area total		34	11	7	16

TABLE 4.—*Existing industrial waste treatment facilities in the coastal area of the Gulf of Mexico* [1]—Continued

1 Type of industry	2 State	3 Number of plants	4 With treatment facilities	5 Without treatment facilities	6 Undetermined
Primary metal industries	Florida				
	Alabama	1			1
	Mississippi				
	Louisiana	1			1
	Texas				
Area total		2			2
Oil production industries	Florida				
	Alabama				
	Mississippi				
	Louisiana	37	6	3	28
	Texas				
Area total		37	6	3	28
Products of petroleum	Florida				
	Alabama				
	Mississippi				
	Louisiana	3		1	2
	Texas				
Area total		3		1	2
Miscellaneous	Florida	1			1
	Alabama	1	0	1	0
	Mississippi	2		1	1
	Louisiana	3			3
	Texas				
Area total		7		2	5
Total		173	19	44	110

[1] Sources lying within 50 miles of the Gulf plus several significant sources lying just outside the 50-mile zone.

DAMAGES TO RESOURCES CAUSED BY POLLUTION

Coastal waters of the Gulf are subjected to pollution directly by discharges from waterfront cities and industries and indirectly through polluted river systems. With this the case, the effects of pollution are not spread uniformly along the coast; they are restricted to localized areas where population and industries are concentrated, where rapid waste dilution is limited by physiographic features, and where exploitable resources occur. It is obvious from this that the susceptible resources include the fin fishes, shrimp, crabs, and oysters that depend upon estuarine existence for at least a part of their life; and near centers of population—the sport fishing and boating waters, bathing beaches and recreational areas, and waterfront property that depreciates as pollution increases.

Available data on sources and kinds of pollution imply notable potentialities for causing damages to resources in restricted areas. In spite of this, observed effects upon the resources have not been of sufficient magnitude to stimulate the required studies aimed at actually evaluating the extent of damage. Surveys and closure of shellfish producing areas because of bacterial contamination give only a fair suggestion of one source of economic loss. Lack of sufficient data makes it impossible to evaluate the full damages from pollution along the Gulf coast.

For purposes of this report the Gulf Coast from Key West to the Rio Grande has been divided into 23 separate drainage areas.[4] Localized pollution damages of some kind or other occur in most of these areas. Almost one-half of them, representing waters of each of the Gulf States, have shellfish areas that are closed to commercial fishing because of pollution. A number of otherwise popular bathing beaches located in at least seven different areas have been made unfit for use. Outright destruction of fish and impairment of sport fishing waters have occurred locally at many points along the coast. Nuisance conditions, losses in property values, effects of sediment deposition, and other more subtle changes that accompany pollution contribute to the total damages.

These impairments of water quality and deleterious effects upon specific resources of the Gulf represent both tangible and intangible values.

[4] See figs. 73 and 74, pp. 562 and 563.

Map No. 1

Sources of Pollution and Existing Treatment Facilities

FIGURE 73.—Sources of pollution and existing treatment facilities.

Map No. 2

Municipal and Industrial Pollution Abatement Needs

FIGURE 74.—Municipal and industrial pollution abatement needs.

It is not possible to place a monetary value upon some of the effects of pollution, particularly those related to public health and welfare. Losses to the fishery, in tourist and resort trade, expenditures for maintaining silted navigation facilities, and perhaps other effects could be expressed in terms of dollars. No estimates of this kind have been made for the entire Gulf, but the total losses undoubtedly would extend into millions of dollars.

The water-pollution picture in each drainage area is summarized in the following pages. Limits of the areas and their numerical designations are shown on figures 73 and 74.

LOWER FLORIDA AREA (1)

In the Lower Florida Area, which extends northward from Key West to include the Caloosahatchee River drainage, the economy depends largely on attracting tourists. Water and climate are chief factors in the attraction. Water resources are used for recreation, agriculture, sport and commercial fishing, and shellfishing. Population is sparse, urban, and has high seasonal fluctuation.

There are four sewered municipalities. Key West has a new sewerage system under construction which will serve about 40,000 people. Inadequately treated sewage is discharged from La Belle with 400 sewered inhabitants.

The following have no treatment facilties:

Municipality:	*Sewered population*
Everglades	300
Fort Myers	11,000

Industry is limited in extent and unimportant to the water-pollution problem.

The tidal estuary of the Caloosahatchee River is adversely affected by pollution from Fort Myers to the mouth. All of the Caloosahatchee River from the west end of the Seaboard Airline Railroad Bridge on the east to a line drawn east across the river on the west from Redfish Point is closed to the taking of shellfish because of pollution.

PEACE RIVER AREA (2)

The Peace River Area includes the west Florida coastal zone from the middle of Pine Island northward to Osprey. Population is predominantly urban. Chief occupations relate to phosphate rock mining, agriculture, and processing crops.

Charlotte Harbor is economically important for sport and commercial fishing, shellfishing, and attraction of a voluminous tourist trade. Upstream the Peace River is used by one small city for domestic water supply.

Raw and poorly treated municipal sewage from five small municipalities, wastes from citrus processing, and finely dispersed clay and matrix materials from phosphate mining activities (Phelps and Barry, 1950) cause pollution of the lower river. There are 4 municipalities with sewer systems serving a total of 8,250 persons. Arcadia, with a sewered population of 3,850, has no sewage treatment facilities. The facilities at the following are inadequate:

Municipality:	*Sewered population*
Wauchula	2,700
Punta Gorda	1,500
Zolfo Springs	300
Fort Meade	2,700

No shellfish areas are closed because of pollution, but the quality of bathing water at Charlotte Harbor beach is affected by sanitary sewage from Punta Gorda. Overall effects of pollution from all sources upon fishery and other resources are not known. The phosphate waste problem has been studied (Specht 1950), and the effects of these wastes, as well as all other wastes entering the stream, are now being studied in a 4-year survey by the Florida State Board of Health in cooperation with the phosphate companies.

TAMPA BAY AREA (3)

The Tampa Bay Area includes the Florida coastal zone from Treasure Island northward to Crystal Bay. The bulk of the population is concentrated in the larger cities of Tampa, St. Petersburg, Sarasota, Clearwater, and Bradenton. Resort trade and widespread recreational use of water for bathing, boating, and fishing are economically important. Water from streams is also used for public water supplies and agricultural purposes. Other notable industries include commercial fishing, phosphate mining, and production of chemicals.

Pollution of the Tampa Bay drainage is caused by municipal discharges serving more than 300,000 persons and by industrial waste from 6 upstream phosphate mines, several citrus canneries, and miscellaneous plants. The larger cities in the resort area either do not have treatment facilities or have inadequate ones.

The following 8 municipalities, with a total sewered population of 29,950, either have no sewage treatment facilities or have inadequate septic tanks:

Municipality:	*Sewered population*
Palmetto	4,000
Pass-a-Grille Beach	900
Palma Cia Park	4,600
Bradenton	12,000
New Port Richie	1,000
Largo	1,000
Virginia Park	3,800
Maryland Manor	2,650

Existing treatment facilities at the following 3 municipalities that serve about 3,000 persons are inadequate:

Municipality:	*Sewered population*
Brooksville	1,000
Crystal River	500
Mulberry	1,600

The following cities have installed, or are installing, adequate sewage treatment plants:

Municipality:	*Sewered population*
Tampa	140,000
Tarpon Springs	5,000
Sarasota	18,000
Plant City	9,000
Dunedin	4,800
Clearwater	10,000
Treasure Island	3,000
Brewster	800
St. Petersburg	61,000
Madeira Beach	5,420
McDill Air Base	6,000

Tampa Bay is grossly polluted, and bathing waters in Clearwater Harbor and St. Joseph Sound have been affected adversely. Several large shellfish producing areas are closed to the taking of shellfish because of pollution. The descriptions of these areas are as follows:

1. Sarasota Bay from Stickney Point Bridge on the south to a line from South Shore of Cow Point to shore of Long Boat Pass.

2. The Manatee River from its mouth to east bank of Braden River; Braden River to a point 1 mile from its mouth.

3. McKay Bay and tributaries, Hillsborough Bay and tributaries, north of a line drawn from the interbay peninsula east to the south bank of the Alafia River.

4. Smacks Bayou; Coffee Pot Bayou; Big Bayou; Little Bayou and waters of Tampa Bay in vicinity of St. Petersburg.

5. All of Clearwater Harbor. That part of St. Joseph Sound south of a line extended west from the center of Ozona.

6. Anclote River and Kramers and Whitcomb Bayous.

7. Both Homosassa and Little Homosassa Rivers and tributaries, Salt River, St. Martins River, excluding Greenleaf Bay, the northern half of Game Creek Bay, and the portion of salt River south of Crystal River to Ozello.

WITHLACOOCHEE RIVER AREA (4)

The Withlacoochee River Area covers the Florida coastal zone from Crystal Bay northward to the middle of Waccasassa Bay. Population is sparse and largely rural. Income is derived chiefly from growing and processing citrus fruits and byproducts. Off the coast, commercial fishing and shellfishing are carried on. The river is used for limited production of hydroelectric power and irrigation.

Because of small populations and large supplies of dilution water damages from municipal and industrial waste pollution are not great. There are only 7 small municipalities with sewerage systems that serve a total of 5,200 persons. Dunellon, with a sewered population of 1,150, has no treatment facilities and Cedar Key, with a sewered population of 400, has inadequate facilities.

Although there are objectionable localized points of pollution in the area, there are no closed shellfish areas. Other resources of the Gulf do not now appear affected.

SUWANNEE RIVER AREA (5)

This area includes the 50-mile coastal zone of the Suwannee River drainage basin fronting on the Gulf between Waccasassa Bay and Horseshoe Cove. This is one of the largest rivers in Florida and is used for sport fishing, public water supplies, waterfowl hunting, and, near the Gulf, for commercial fishing and shellfishing. Population is predominantly rural. Products of the area include corn, tobacco, peanuts, pecans, tung oil, lumber, and raw material for naval stores extraction. There are no noteworthy industrial operations.

Three small unsewered municipalities will need adequate treatment facilities of some kind whenever sewerage systems are developed.

Damages to either fresh water or marine resources are not defined but appear unlikely, or of little consequence.

OCHLOCKONEE RIVER AREA (6)

The Ochlockonee River Area extends along the Gulf coast from Horseshoe Cove to East Bay near Apalachicola. The coastal towns are tourist, resort, and fishing camp centers. St. Marks, Carrabelle, and Panacea are ports of some importance. The bulk of the population is employed in agriculture and logging, and industry is of minor importance.

Sport and commercial fishing and shellfishing, recreation, and shipping are the principal water uses.

Of 9 municipalities, with almost 33,000 sewered inhabitants, only Tallahassee and Foley do not need improvements in sewage disposal. Four small municipalities have no effective treatment facilities:

Municipality:	*Sewered population*
Quincy	3,300
Perry	1,200
Havana	200
Monticello	1,500

Two others, with a total sewered population of 1,500, have inadequate treatment:

Municipality:	*Sewered population*
Dale Mabry	1,000
Carrabelle	500

The bay area adjacent to Carrabelle is polluted to some degree apparently by shipping in the port of Carrabelle and perhaps also by drainage through New and Crooked Rivers. All of the Spring Creek area north of a line extended across the mouth of the creek in southeast to northwest direction is closed to taking shellfish because of pollution.

APALACHICOLA RIVER AREA (7)

The Apalachicola River Area fronts on the Gulf from East Bay westward to Beacon Hill. Population is sparse and mainly rural. Economic activity includes significant agriculture such as production of peanuts, cotton, corn, tobacco, hogs, and cattle, and cutting of timber near the coast. A sulphate paper mill is located at Port St. Joe.

Waters of the area are popular for game fishing, bathing, boating, and other recreation. Commercial fishing and shellfishing are very important sources of income. Catches of shrimp in Apalachicola Bay and the coastal waters from Cape St. George to St. Joseph's Point make Apalachicola a principal production center.

The area has 2 sewered municipalities with a connected population of 3,500 persons. Port St. Joe has treatment facilities of adequate capacity, but these need improved operation; the facilities at Apalachicola are inadequate.

Near the mouth of the Apalachicola River the waters are among the most productive of shellfish in the entire Gulf. Because of sewage pollution part of these waters have been closed to commercial shellfishing. They are described as follows (Wakefield 1948): Bounded on the west by a line from the mainland to the eastern tip of St. Vincent Island, this line being sighted from the white beacon "f" through the eastern tip of St. Vincent Island; thence easterly to beacon "2"; thence easterly to beacon "52"; thence north through the western tip of Cat Point; to the mainland; and all of the area bounded by the mouths of the Apalachicola, Little St. Marks, St. Marks, and East Rivers.

Pollution in St. Joseph's Bay is caused by a poorly operated municipal treatment plant at Port St. Joe and from the paper mill at the same location.

CHOCTAWHATCHEE RIVER AREA (8)

The Choctawhatchee River Area extends along the Gulf coast from St. Joseph's Point westward to Mary Esther. Within 50 miles of the coast uncleared timber land is used for cattle grazing. Commercial fishing and shellfishing are important along the coast. Beyond 50 miles, agriculture predominates. Tourist trade, sport fishing, and related recreational activities are important sources of income related to water resources.

Six municipalities, four of which have a total sewered population of 19,000, have adequate sewage treatment facilities.[5] DeFuniak Springs discharges raw sewage from 1,000 persons, and Lynnhaven has inadequate facilities.

Only minor pollution problems occur over most of the area, but discharges of municipal sewage from the Panama City-Lynn Haven area have limited the utility of recreational waters in St. Andrew's Bay adjacent to Panama City, the

[5] The remaining two municipalities are military establishments for which data on populations served by sewers are not available.

south shore of North Bay near Lynn Haven, and in East Bay. The following areas are also closed to commercial shellfishing:

North Bay: (Fanning Bayou) that part north of the mouth of each of the three prongs. (Upper East) all of that part south of a line extending west from Deer Point through Mill Point to the south point of Newmans Bayou and bounded on the west by a line extending south to Little Oyster Bar Point. (Lower South) all of that part south of a line extending east from Shell Point to the south shore of Coose Bayou.

St. Andrew Bay: All of the bay from Hathaway Bridge on the west to DuPont Bridge on the east excepting that part on the Gulfside of a line extending from Bear Point to Redfish Point.

Wastes from a sulphate pulp and paper mill near Panama City caused local conditions inimical to aquatic life as recently as 1950 (Anonymous 1950), but remedial action has since been taken by the industry.

PERDIDO-ESCAMBIA AREA (9)

Perdido–Escambia Area extends westward from Mary Esther, Florida, to the vicinity of Bon Secour, Alabama. Pensacola is the chief population and industrial center and an important seaport which also harbors commercial fishing fleets. Production of livestock and timber are principal nonurban activities. Water resources of the coastal area relate to sport and commercial fisheries, oyster production, bathing, and recreation.

Pensacola, which discharges partially treated sewage from a population of 35,000 persons into Pensacola Bay, is the chief source of sewage pollution. Discharges from 2 other inadequate municipal treatment plants that serve about 3,700 persons reach waters of the area also:

Municipality:	*Sewered population*
Moreno Court	3,000
Robertsdale, Alabama	700

Flomaton, with 1,000 sewered inhabitants, has no treatment facilities.

Because of sewage pollution large areas have been closed to the production of shellfish. They are described as follows:

1. All of Pensacola Bay west of a line drawn due south from Gulf Point to the south shore of the bay–Bayou Texar and Bayou Chico.

2. That portion of Escambia Bay north of the Louisville and Nashville Railroad Bridge.

3. All of Blackwater Bay north of a line drawn west through Escribasso Point.

The quality of bathing waters also has been affected. This is particularly true in certain parts of Pensacola Bay, in Bayou Grande, Bayou Chico, and Bayou Texar.

Industrial wastes from breweries, dairies, rendering plants, a large naval stores plant, and a paper mill have caused objectionable pollution conditions.

Paper mill wastes have made Elevenmile Creek unfit for fish despite remedial action by the industry (Anonymous 1950). Conditions in the bay prevent growing shellfish that would have a great potential annual value (Phelps and Barry 1950).

MOBILE BAY AREA (10)

The Mobile Bay Area includes Bon Secour Bay and extends westward to Isle Aux Herbes. Population is concentrated at Mobile which forms the center of an industrial area at the head of Mobile Bay. Ship building and repair, pulp and paper making, and lumbering are prominent. In addition to serving as a navigation waterway, Mobile Bay is used extensively for commercial fishing, oyster production, recreation, and a wintering area of waterfowl. Hunting is a popular sport there. It is also one of the principal shrimp fishing grounds of Alabama.

Adequate facilities for disposal of municipal sewage now serve 30 percent of the sewered population. The City of Mobile has purchased a site and plans are under preparation for a sewage treatment plant which will serve approximately 85,000 people. The Eslava Treatment Plant for the City of Mobile is being enlarged to three times its present capacity and will provide treatment for approximately 42,000. Pritchard has a new treatment plant under construction which will serve 10,000 people. Improvements have been made at the Chickasaw Plant which is now satisfactorily treating the sewage from 10,300 people. Industrial wastes including both organic and inorganic wastes of unknown quantities are discharged into the Bay.

Pollution has affected bathing and other recreational waters in various parts of the bay. A number of areas have been closed to commercial

shellfishing because of pollution. These are described as follows:

1. All of Bon Secour River lying upstream from a line extending due north from the east bank at the inlet to Oyster Bay from said Bon Secour River.

2. Bayou Labatre and the coastline area immediately adjacent to its mouth.

3. Bayou Coden and the coastline area immediately adjacent to its mouth.

4. Areas affected by pollution from Mobile River including Upper Mobile Bay near the mouth of the river. Dog River, the shoreline in the vicinity of Fairhope and Fish Rivers do not involve shellfish producing areas because no oyster reefs exist in the immediate vicinity.

Protection of the water resources from the damaging effects of pollution can be accomplished by providing sewage treatment facilities for 3 municipalities serving approximately 100,000 persons. Information is not conclusive in regard to the effects of industrial wastes on shellfish production.

PASCAGOULA RIVER AREA (11)

The Pascagoula River Area covers the coastal zone from Isle Aux Herbes in Alabama westward to Bay St. Louis, Mississippi. Principal cities are Pascagoula, Ocean Springs, Biloxi, Gulfport, Long Beach, and Pass Christian. In addition to a thriving winter tourist patronage along the coast, economy of the area depends upon processing natural resources. These include lumber, naval stores, paper, and sea food. Recreational uses of watercourses, such as fishing, hunting, and boating, are of major importance. Coastal waters yield fish, shrimp, crabs, and oysters. Biloxi is the principal shrimp and oyster landing port of Mississippi.

A total sewered population of approximately 54,000 is distributed among seven municipalities or institutions. Gulfport, which has a sewerage system serving only a small part of the City, has extended its sewers to include most of the town. The City has acquired and is now using the existing facilities of Gulfport Field for the treatment of sewage. Although most cities have sewage treatment plants, sewage pollution is sufficiently serious in some areas to prohibit commercial shellfishing. Closed areas are described as follows:

1. The area included in Pascagoula River from a point 1 mile above Pascagoula River toll bridge to a point 2 miles outward from the mouth of the river and within the east and west boundaries of the Pascagoula River channel.

2. The Back Bay of Biloxi north and west of Highway 90 bridge extending from Biloxi, Mississippi, to Ocean Springs, Mississippi.

3. That portion of Biloxi Bay included between the U. S. Highway No. 90 bridge across Biloxi Bay and a straight line across the Bay determined at its northeast extremity by the water tower in Ocean Springs and its southwest extremity by Flashing Light No. 31 off the eastern tip of the Biloxi Peninsula, which line shall then proceed in a westerly direction to the northwestern end of Deer Island, and including the area fronting the city of Biloxi from the Biloxi USO Building to the most easterly point of Biloxi Peninsula at the U. S. Coast Guard Base, and lying between the main shore line and the line from Flashing Light No. 31 to the northwestern end of Deer Island. Also included is the area commonly referred to as the "Ocean Spring Small Craft Harbor" from the Biloxi Bay shoreline inward to the upper extremity of this harbor.

4. The area bounded on the north by that portion of the Gulfport shore line of Mississippi Sound between its intersection with the extension of 42d Avenue South in Gulfport, and the east boundary of the United States Veterans Hospital property; on the west by a line running south 2 miles from 42d Avenue extended; on the east by a line running south two miles from the east boundary of the United States Veterans Hospital property; and on the south by a line running parallel to the shoreline and 2 miles therefrom connecting with the outer ends of the east and west boundary lines.

Industrial wastes of various kinds are discharged to the area's waters in sufficient quantities to cause local problems. Bayou Bernard, which empties into Back Bay near Biloxi, has had periodic killings of fish from industrial waste pollution (Anonymous 1950).[6] A sports fishery has been damaged in tributary waters adjacent to Back Bay at Gulfport. Bathing waters have been affected at Back Bay and Biloxi Bay near Biloxi and at the beach at Pascagoula.

[6] From a summary report on the Pascagoula River Basin prepared by Mississippi State Board of Health. Unpublished.

PEARL RIVER AREA (12)

The Pearl River Area includes drainage from parts of Mississippi and Louisiana and fronts on the Gulf between Bay St. Louis and a point 5 miles west of the Louisville and Nashville Railroad Bridge crossing the Rigolets. Population is sparse. Principal population and industrial centers are Bogalusa and Franklinton, Louisiana, which are located inland. Industrial operations include production of naval stores and other chemical products, pulp and paper, primary metals and processed foods. A number of oil and gas fields are located in the lower part of the drainage basin.

Waters of Mississippi Sound and Lake Borgne are used extensively for sport fishing, bathing, boating, and other recreation. They are also fished commercially for fin fish, shrimp, and oysters.

There are no sewered municipalities on the Gulf coast in this area. Bogalusa, with a sewered population of 10,000, discharges untreated sewage to the Pearl River about 50 miles above the mouth. Industrial wastes of various kinds are discharged at Bogalusa, Franklinton, and Picayune. Although pollution occurs upstream in the watercourses, no shellfish areas downstream are closed to commercial fishing. Effects upon other resources of the Gulf are unknown.

LOWER MISSISSIPPI RIVER AREA (13)

The Lower Mississippi River Area includes the section south of Baton Rouge that is bounded on the east by the Pearl River Basin and on the west by the East Atchafalaya Basin Protection Levee southward to Morgan City and from this point southward to Atchafalaya Bay. Because of levees no appreciable surface drainage reaches the Mississippi River. Drainage east of the Mississippi River and north of New Orleans drains to the Gulf through Lake Pontchartrain. Drainage west of the Mississippi is away from the river and southerly to the Gulf.

The water of the Mississippi entering the area already has passed through cycles of pollution and recovery from distant sources of pollution. The effects of such pollution upon the Gulf are not significant. Drainage from erodible lands through which the river flows already have given it, at this point, an annual sediment load of one-half billion tons.

New Orleans is the chief population, industrial and marketing center and also an important port. Land use is principally agricultural. Petroleum production and refining, chemical manufacture, and processing of sugar, foods, seafood, menhaden, cottonseed, and wood are principal industrial activities. Fresh water resources are important for public and industrial water supplies. The coastal waters are used for sport fishing and other recreation and are a rich source of sea food. Chandeleur and Breton Sounds and Barataria Bay are fished extensively for shrimp. Much of the coastal area along the delta and westward is swampland cut by complicated sluggish watercourses. Large areas are set aside as wildfowl refuges, but the swamplands also serve as rich muskrat trapping grounds.

Of 15 sewered municipalities in the area, 5 discharge sewage without treatment. The largest is New Orleans, with a sewered population of 582,000, which pumps the sewage to the Mississippi River. The others are the following:

Municipality:	*Sewered population*
Plaquemine	5,740
St. Bernard Sewage District	------
Donaldsonville	4,500
Gretna	11,000

Three other municipalities have sewage treatment facilities that are inadequate:

Municipality:	*Sewered population*
Houma	10,000
Covington	3,500
Slidell	2,000

At least 22 industrial plants discharge untreated wastes. Among them are at least 19 sugar plants distributed in the area. Pollution prevention measures are in operation at an oil refinery upstream at Baton Rouge and at Norco (Anonymous 1951b).

Because of large quantities of dilution water serious effects of pollution are principally localized near concentrations of industry. No shellfish areas are closed to commercial fishing because of pollution.

ATCHAFALAYA RIVER AREA (14)

The Atchafalaya River Area includes the drainage southward from Lafayette and fronts on the Gulf from Caillou Bay to Grand Chenier. The lower parts of the Morganza and related floodway systems drain through the area. Agriculture is a

major activity with rice, cotton, and sugarcane as principal crops. Oil fields and sugar processing plants are scattered outside the floodway area. Principal cities are Crowley, Lafayette, and New Iberia. Water resources are used for irrigating rice, for navigation, and sport and commercial fishing. Caillou, Atchafalaya, and Vermillion Bays are fished extensively for shrimp. Coastal swamps are used for hunting, muskrat trapping, and wildfowl refuges.

Twelve municipalities have sewerage systems that serve almost 80,000 persons. Nine have adequate sewage disposal facilities, Jennings with 7,300 persons has none, and the facilities at the following are either inadequate or poorly operated:

Municipality:	*Sewered population*
Abbeville	9,000
Jeanerette	4,000

Industrial waste pollution is caused principally by sugar plant wastes and oil field brines. Large quantities of organic matter are discharged during the harvest season from 22 cane sugar mills that have a combined daily capacity of 31,000 tons of sugar. More than 11,000 barrels of brine wastes per day result from oil field operations. Although 65 to 70 percent of the salt brines are disposed of adequately by reinjection, appreciable quantities still enter surface waters.

No shellfish areas are closed to commercial fishing because of sewage pollution. During the sugar season local nuisances result from sugar mill wastes. In the past, brine wastes have interfered with the use of rice irrigation water, but at the present time, orders issued by the Stream Control Commission forbid deposition of brines into irrigation waters during certain times of the year.

CALCASIEU RIVER AREA (15)

The Calcasieu River Area includes the lower 50 miles of the narrow Calcasieu Basin. It fronts on the Gulf between Grand Chenier and Johnson's Bayou. The area is important for production of rice and a number of minor crops, has about 20 oil fields, and industrial activities that include petroleum processing, ginning cotton, production of pulp and paper, and food processing. Lake Charles is the principal city. Uses of fresh water include rice irrigation, industrial use by oil refineries and paper mills, and navigation below Lake Charles. Muskrat trapping and farming are important in marshes south of Lake Charles. Shrimp and fish are taken from the offshore waters.

Lake Charles, with a sewered population of 54,000, and Maplewood with 2,500, have municipal sewage treatment facilities. One small community that is located some distance inland has inadequate facilities, and Oakdale, also inland, discharges untreated municipal sewage. The Lower Calcasieu River is also subject to considerable pollution from ship traffic and from periodic flooding of land areas at the small communities of Cameron and Hackberry where pit privies are common. Principal industrial wastes come from oil fields, two oil refineries, two chemical plants, and a fish meal company.

Because of sewage pollution, the entire Calcasieu River and its tributaries are closed to commercial shellfishing. During periods of low flow, wastes from oil refineries and other industries have caused oxygen depletion in parts of the Calcasieu River.

SABINE RIVER AREA (16)

The area includes parts of Louisiana and Texas in the Sabine River drainage basin, the eastern half of Sabine Lake and its pass to the Gulf. The largest city is Orange, Texas. Cattle and rice are principal agricultural products. Oil wells are numerous. Industrial processing includes petroleum, chemicals, and food. Fresh water is used extensively for rice irrigation, industrial water supplies, and navigation. Fish and shrimp are taken from the offshore waters.

Sewered municipalities are Orange, Newton, and Kirbyville, Texas. Their sewer systems serve 25,000 persons. The existing facilities at these municipalities have adequate capacity. Considerable pollution comes from oil-well brines and sediment loads from erosion.

The Sabine and Neches Rivers together carry an annual silt load of about 7 million tons into Sabine Lake. During the past 75 years, ocean-going shipping on the lake has become restricted to the confined channel of the Intercoastal Waterway which is maintained by dredging. Oyster reefs in Sabine Lake were destroyed long ago by siltation.

NECHES RIVER AREA (17)

The Neches River Area includes the drainage from Silsbee downstream and extends along the

Gulf from the middle of Sabine Lake to High Island. Beaumont and Port Arthur are largest of the 9 cities with more than 80 percent of the urban population. Petroleum, gas, cotton, and other farm products are the basic materials for industry which is concentrated near these cities. Water use by industry is heavy and important; tremendous quantities are used for rice irrigation also. Coastal waters are used for sport fishing and other recreation. Fish and shrimp are taken commercially offshore.

Total organic pollution load from all sources in the area is estimated at 750,000 population equivalent. There are 9 municipalities that have sewer systems serving a total of 173,000 persons. The following municipalities are without sewage treatment facilities:

Municipality:	*Sewered population*
Groves	2, 470
Port Neches	5, 450
Lakeview	3, 080
Griffing Park	2, 100
Port Arthur	57, 400

There are also wastes from industries of various kinds and salt brines from oil fields. Soil erosion over the drainage area has resulted in damaging silt deposits in both the Neches River and Sabine Lake. (See Sabine River Area.) The river had a natural 60-foot deep channel upstream to Beaumont in 1876 but now requires continuous dredging to maintain a 25-foot channel.

At times fishing has been damaged by effects of organic waste pollution. Although salt brines have occasional effects upon irrigation water, effects upon resources of the Gulf are not known.

TRINITY RIVER AREA (18)

The Trinity River Area includes drainage from Livingston downstream on the Trinity River, from Humble downstream on the San Jacinto, and drainage from the area surrounding Galveston Bay. The area fronts on the Gulf between High Island and the southern tip of West Bay. The drainage basin is predominantly agricultural except for the Houston-Galveston area where a growing variety of manufacturing industries has been developed. About 65 percent of the population of the Texas Gulf area is concentrated about this industrial development. Petroleum and chemical industries are prominent.

Watercourses are used for public and industrial water supplies; Galveston Bay for navigation and for fishing to a limited degree. In the vicinity of Galveston, Gulf waters are popular for sport fishing, bathing, boating, and other recreation. Galveston is an important shrimp landing port.

All but one of the sewered municipalities, with systems serving about 1 million persons, have sewage treatment facilities. Most of these are adequate. Although Galveston now has no treatment facilities for a connected population of 70,000, a plant is under construction. Because of pollution from municipal wastes, that area of Galveston Bay lying between a line extending from Texas City along the dike to the point of the ferry landing on Bolivar Peninsula as a northern boundary and the Galveston causeway as a western boundary is closed to the taking of shellfish. However, it is believed very few, if any, shellfish are actually to be found in this area. Industrial wastes also contribute to the pollution problem, although there is little specific information on wastes from the various industries or oil fields. Galveston Bay receives an annual silt load of 8.1 million tons from the Trinity River and 1.2 million tons from the San Jacinto.

There has been a spectacular decline in Galveston Bay fishery resources during the past 60 years Since 1890 the catch dropped from more than a million pounds to only 336 pounds in 1948. Pollution is considered an important contributory factor. At the present time an extensive pollution survey is being made of Galveston County waters by the Texas State Department of Health in cooperation with Galveston County. Fishing has been seriously damaged in Buffalo Bayou by sewage from Houston.

BRAZOS RIVER AREA (19)

The Brazos River Area includes drainage of the Brazos and San Bernard Rivers from Rosenberg toward the Gulf. At the coast, the area extends between West Bay and Matagorda Bay. Population is fairly low. Rosenberg, Bay City, and Freeport are the principal cities. Industry of the area has developed around petroleum and agricultural products. Irrigation of rice and industrial and municipal water supplies are the principal uses of fresh water. Coastal waters are used for fishing and recreation. Freeport is an important shrimp landing port.

Most of the municipalities now have sewage treatment facilities, but West Columbia, Velasco,

and Freeport do not. This results in the discharge of raw sewage from 10,000 persons. The following municipalities have inadequate sewage treatment facilities:

Municipality:	*Sewered population*
Richmond	2,000
Brazoria	1,000

Pollution also is caused by brine wastes and wastes from a number of industrial plants. Large sulfur workings and a plant for recovering chemicals from salt water are located at Freeport.

The Brazos River once entered an estuary much larger than Galveston Bay but now flows directly to the Gulf after having filled the estuary with silt. The river carries an estimated annual silt load of 35.3 million tons despite the small drainage area.

Water pollution damages to resources of the area are not well defined. No shellfish areas are closed because of pollution, but periodic fish losses near Freeport are believed caused by discharges of caustic wastes from an industry located there.

COLORADO RIVER AREA (20)

The Colorado River Area includes the lowermost drainage of the Colorado River and the part of Matagorda Bay lying northeastward from Tres Palacios Bay. Matagorda at tidewater and Wharton 47 miles upstream are the only sewered municipalities. Economic activity is based upon petroleum and agriculture, but industrial development is limited, and the few existing factories are scattered. Fresh water is used for domestic and industrial water supplies and for irrigation. Matagorda Bay is used for sport fishing, waterfowl hunting, boating, and other recreation. Fish and shrimp are taken commercially here and off shore.

Untreated sewage from 4,500 persons at Wharton is the only municipal source of pollution. Silt is the major cause of pollution. Because of upstream impoundments, the river now carries to the Gulf a silt load acquired mainly in the lower 245 miles of its course. Annual load prior to 1941 was estimated at 8.9 million tons. Silt is reported to have all but destroyed some six or seven thousand acres of oyster reefs near Matagorda. None of the remaining shellfish areas are closed because of pollution. Like the Brazos River the Colorado has formed a delta to the Gulf and overflows to Matagorda Bay only at flood flows.

GUADALUPE RIVER AREA (21)

The area includes drainage of the Navidad, Lavaca, Guadalupe, and San Antonio Rivers, and the bay areas and coastal waters from Tres Palacios Bay to Hines Bay. Victoria, El Campo, and Port Lavaca are the principal cities. Cotton farming and production of oil and gas, especially in the coastal area, are chief economic activities. A large aluminum reduction plant is located at Port Lavaca. Water uses include municipal and industrial water supplies, irrigation, and recreation. Oyster reefs of commercial importance are located in Espiritu Bay and Tres Palacios Bay near O'Connor. Bay areas are important for sport fishing and hunting of waterfowl. Fish and shrimp are taken commercially in the bays and offshore waters. Palacios and Port Lavaca are important shrimp landing ports.

There are 11 municipalities with sewer systems that serve a total of 40,000 persons. All of these municipalities have sewage treatment facilities, but facilities of the following are inadequate:

Municipality:	*Sewered population*
Ganado	1,350
Edna	3,600
Goliad	800

No shellfish areas are closed to commercial fishing because of pollution. Except for oil-field brines, industrial wastes are not a serious problem. Corrective action instigated by the pollution control agencies is proving quite effective in reducing the effects of brine pollution.

Lavaca Bay receives the silt loads of the Lavaca and Navidad Rivers and shorter Karon-Lavaca and Tres Palacios Creeks. The Lavaca, alone, carries an average annual silt load of more than 200,000 tons. Guadalupe and San Antonio Rivers discharge silt into San Antonio Bay: the Guadalupe at an average annual rate of 600,000 tons and the San Antonio at least 700,000 tons.

Effects of pollution upon resources of the adjacent area of the Gulf are not known.

NUECES RIVER AREA (22)

The Nueces River Area includes drainage of Mission, Aransas, and Nueces Rivers. It fronts on the Gulf between Hines Bay and Corpus Christi Pass. Principal cities are Corpus Christi,

Beeville, and Robstown. With exception of the vicinity of Corpus Christi, the area is sparsely populated, with farming and cattle ranching the chief activities. Sulfur and rock asphalt are produced and processed, and oil production is increasing. A large corn products refinery and a synthetic fabrics plant are located in the Corpus Christi area. Fresh water resources are used extensively for municipal and industrial water supplies, stock-watering, and irrigation. Oyster reefs are located in Nueces, Copano, Aransas, and Mesquite Bays. The area is popular for sport fishing, waterfowl hunting, and boating. Aransas Pass and Rockport are important shrimp landing ports.

There are 12 sewered municipalities with a total sewered population of 137,500 of which 100,000 are in metropolitan Corpus Christi. Although all sewered municipalities provide sewage treatment, the facilities at the following three are inadequate:

Municipality:	*Sewered population*
Refugio	3,700
Odem	1,200
Ingleside	150

Nueces Bay was closed to commercial oystering about 20 years ago because of raw sewage discharges at Corpus Christi. Improved facilities for sewage treatment now in operation and elimination of waterfront privies have permitted resumption of oyster marketing. There are now no areas closed to commercial fishing.

Large quantities of oil-field brines are evaporated in ponds or injected underground. Some not so treated have caused pollution of Mission Creek and Copano Bay. Wastes from a synthetic fabrics plant at Kingsville were suspected of causing a fish kill. Caustic soda from a chemical plant has, on occasion, affected waters in a turning basin near Corpus Christi. This problem is receiving attention by the industry. The extent of damage from these conditions is not known.

LOWER RIO GRANDE AREA (23)

The Lower Rio Grande Area is the coastal zone from Corpus Christi Pass to the International Boundary. It includes drainage of a number of creeks, Arroyo Colorado, and the Rio Grande River. The northern portion is dry, sparsely populated, and utilized for cattle ranching; the southern part is in the "Magic Valley" with its widespread irrigation, semitropical climate, and tremendous agricultural development. Processing of citrus fruits and vegetables is a major industry along with fish and shellfish processing. Brownsville, Harlingen, Alice, and McAllen are principal cities. Tourist trade is a major factor in the area's economy during the winter months. Fresh water resources are used extensively for irrigation. The Arroyo Colorado serves as a wasteway for surplus Rio Grande water, an irrigation drain, and as a waste disposal canal to Laguna Madre. About 200 fishing boats operate from the mouth of the river. There are oyster reefs in South Bay. Coastal waters are also used for sport fishing and recreation.

The 27 sewered municipalities have a total connected population of 146,300, and all have treatment facilities. The facilities of 9 municipalities serving 15,300 persons are inadequate:

Municipality:	*Sewered population*
San Diego	1,800
Orange Grove	550
Aqua Dulce	100
Bishop	2,000
Mercedes	500
La Feria	1,470
Edcouch	500
Rio Hondo	400
San Benito	8,000

Only two municipalities discharge treatment plant effluents to the Rio Grande, most others to Arroyo Colorado. Industrial wastes come from numerous fruit, vegetable, and sea food canneries and quick-freeze plants, oil refineries, a chemical plant, a large candy and gum factory, and castor and cottonseed processing plants.

The Arroyo Colorado, at times, is heavily overloaded with sewage and industrial wastes. Effects upon resources of Laguna Madre or the Gulf are not known. The oyster beds in South Bay are 50 miles distant from the mouth of Arroyo Colorado and well protected by distance from the discharged wastes.

THE GULF COAST OF THE REPUBLIC OF MEXICO

In general, the area draining to the Gulf is sparsely populated. Land is used largely for grazing, lumbering, and agriculture. The oil industry is the only one of significance with respect to water pollution. Fishing for fin fish, shrimp, and oysters are important local industries along the coast. The oyster producing capacity of

Mexican waters has not been developed thoroughly because of lack of markets. Local beaches are used extensively for bathing and, even near the cities, the Gulf waters are clear and inviting.

Except for Tampico, Veracruz, Villa Hermosa, and Coatzacoalcos, domestic sewage is disposed of on an individual basis. The effects of such disposal upon the Gulf and its estuaries is negligible. At Tampico untreated municipal sewage is discharged to the Panuco River which provides adequate dilution to prevent nuisances. Because of a peculiar combination of tides and currents this sewage has contaminated parts of Laguna Vieja beyond acceptable limits for oyster harvesting. At Veracruz a primary sewage treatment plant was constructed and placed in operation in 1950. A few sewer outlets are not as yet connected to the treatment plant.

Loading of crude oil into ships at Tampico, Tuxpan, and Coatzacoalcos, on occasion, has resulted in accidental spills that have fouled beaches near these points. The offending parties have been cooperative in preventing recurrences. This is the only known industrial waste problem on the Gulf, and there are no records of injury to fish or other aquatic life.

Silt deposition is the greatest pollution problem on the Mexican Gulf Coast. Silt and sand carried by the Panuco and Grijalva Rivers clog the harbors at Tampico and Alvaro Obregon, respectively, and necessitate dredging to permit navigation. From north to south the silt carrying rivers of Mexico discharging along the Gulf coast are: Soto la Marina, Barbarena, Panuco, Tuxpan, Cazones, Nautla, Tecolatia, Actopan, Misantla, Boca del Rio, Papaloapan, Coatzacoalcos, Tonala, Nuevo San Filipe, Santana, Cuxcucha, Grijalva, and San Pedro. Many of these streams discharge to brackish estuaries which contain oyster reefs. Undoubtedly the deposition of silt will destroy the oyster reefs which are a valuable natural resource.

Because of the near nonexistence of sewage and industrial waste pollution in the Gulf coast area there is no antipollution campaign in Mexico. Federal law regarding pollution is very brief and consists of a paragraph or two in the Sanitary Code which forbids the discharge into waters of materials harmful to health and navigation. Under the Sanitary Code detailed regulations could be drawn up for controlling pollution, but this has not been necessary as yet. The Federal Health Department (Salubridad) and Federal Harbor Police (Marina) are the agencies charged with pollution control; their activities along this line are largely concerned with handling complaints. Principal complaints concern the oil pollution previously mentioned. There is no routine determination of water quality or the amounts of pollution except in the Tampico area where the health department has an interest in the bacterial quality of oyster-producing waters. The several Mexican States could, if so inclined, promulgate and enforce water pollution control laws.

For the past several years Mexico has discussed soil conservation, and some beginnings of a working program have developed which in time will reduce the amount of silt carried to the Gulf.

From the standpoint of organic pollution of Gulf waters the program carried out in Mexico is adequate to handle present conditions, although from a conservation and public health view some soil conservation and general sanitation practices could be improved. It can be safely said that when Mexico has a real need for an antipollution campaign it will be forthcoming.

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